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AN ECOLOGICAL STUDY OF GRASSLANDS AT LOW
ELEVATIONS IN BANFF, JASPER AND
WATERTON LAKES NATIONAL PARKS

by



PAUL WILLIAM STRINGER

A THESIS

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The undersigned certify that they have read,
and recommend to the Faculty of Graduate Studies for
acceptance, a thesis entitled "An Ecological Study of
Grasslands at Low Elevations in Banff, Jasper and
Waterton Lakes National Parks" submitted by Paul William
Stringer in partial fulfilment of the requirements for
the degree of Doctor of Philosophy.

ABSTRACT

In 1967, 51 stands representative of the grasslands at low elevations in Banff, Jasper, and Waterton Lakes National Parks were selected by means of airphoto and ground surveys. Quantitative sampling methods were used to describe the floristic composition and vegetation structure of these grasslands and physical and biotic environmental factors operating on them.

In 1968, 20 additional stands were sampled quantitatively at three intensive study sites within the two major grassland types, and the relations between vegetation and physical habitat analysed by simple correlation and multiple regression. Standing crop studies were carried out at representative locations. Three environmental stations were set up in 1967, one in each Park.

Three-dimensional ordination based on vegetative similarity detected correlations between the grassland composition and structure and the measured environmental factors; indicated a discontinuity between the Waterton and Banff-Jasper stands; and suggested several grassland types.

Cluster analysis verified this discontinuity, clarified the classification of the 71 stands, and indicated the following grassland types: mesophytic *Festuca-Danthonia* Prairie, the major grassland type in Waterton, characterised by a high species diversity and standing crop, and by the Dominance of *Danthonia parryi*, *Festuca idahoensis*, *F. scabrella*, *Galium boreale* and *Lupinus sericeus*;

xerophytic *Koeleria-Calamagrostis montanensis* Grassland, most prominent in the Athabasca River valley in Jasper, and characterised by low species diversity and standing crop, by the Dominance of *Calamagrostis montanensis*, *Koeleria cristata*, *Antennaria nitida*, *Artemisia frigida* and *Astragalus striatus*, by heavy grazing by elk, and a dry climate; low-lying grass and sedge meadows in Waterton, dominated by introduced hay species; *Poa-Hordeum jubatum* Grasslands on clay soils in certain narrow valleys in Jasper; xerophytic *Koeleria-Geum triflorum* Grasslands, heavily grazed by horses and elk, and dominated by *Koeleria cristata*, *Helictotrichon hookeri*, *Antennaria nitida* and *Geum triflorum*; *Stipa richardsonii* Subalpine Grasslands in small parks with well-defined shrub stratum and dominated by *Stipa richardsonii*, *Danthonia intermedia*, *Penstemon confertus* and forest understory species; *Elymus innovatus* Subalpine Shrub Savanna, maintained by snow slides or rock falls, dominated by forest understory species, and with a well-defined shrub stratum.

The first two types are the most extensive. The other types are of much smaller extent and their statuses as distinct grassland types are only tentative.

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INTRODUCTION

Banff, Jasper and Waterton Lakes National Parks are in west and south-west Alberta, east of the Continental Divide, in the Main and East Ranges of the Rocky Mountains or their foothills.

Banff and Jasper Parks are completely within the mountain ranges and in area are 2,585 and 4,200 square miles respectively. To a large extent, the dominant vegetations of these areas are coniferous evergreen forest in the montane and subalpine zones and tundra in the alpine zone (Rowe, 1959). Grassland vegetation covers only a few square miles on the bottoms of the larger river valleys, such as those of the Athabasca and Brazeau in Jasper and the Bow and Red Deer in Banff. Even where most abundant, these low-elevation grasslands are neither extensive nor continuous, but they form a very distinctive component of the vegetation mosaics in the valley bottoms of the two Parks. On the basis of the normal zonal sequence in the Rocky Mountains (Oosting, 1956), it was estimated that the lower elevational limits of the montane zone are close to or below the bottoms of the main valleys of Banff and Jasper Parks. The basal plains of the Athabasca and Bow rivers are considered as being in "the montane forest region" and their vegetation is classified as an association of Douglas fir (*Pseudotsuga menziesii* var. *glauca*)¹ and lodgepole pine (*Pinus contorta* var.

¹ Vascular plant nomenclature follows Moss (1959).

latifolia) (Rowe, 1959). The low-elevation grasslands in Banff and Jasper National Parks occupy only locally favorable areas on these basal plains or on lower, S-facing slopes.

Waterton Lakes National Park is only 204 square miles in extent but approximately ten per cent of this area is grassland. The western and southern parts of the Park are in the Rocky Mountains and have coniferous evergreen forest and alpine tundra vegetation. However, the lower limits of the montane zone do not seem to reach the basal plains of the two main river valleys, those of the Waterton and Belly rivers, and many of the E and N parts are in lower-elevation foothills occupied by extensive areas of prairie (*sensu* Weaver and Clements, 1938) and by a mosaic of poplar forest (mostly *Populus tremuloides*), coniferous-poplar forest, scrub, meadow and marsh.

Thus, there is a difference between the scattered, relatively small areas of predominantly montane grassland in Banff and Jasper Parks and the extensive, semi-continuous areas of prairie (*sensu* Weaver and Clements, 1938) in Waterton Lakes Park at ecologically lower elevations.

There have been no comprehensive plant ecological studies of grasslands in these three Parks, but Flook (1965), Cowan (1947) and Pfeiffer (1948) have described the range relationships of ungulates in the Banff and Jasper grasslands. Breitung (1957) compiled a useful list of plants of Waterton Park with brief notes on their distribution.

Coupland (1961), in his reconsideration of the grassland classifications in the Northern Great Plains of North America, states that "natural grasslands of the four western provinces of Canada are comprised of four associations (in the Clementsian sense) namely: The Mixed Prairie (*Stipa-Bouteloua*) Association, the True Prairie (*Stipa-Sporobolus*) Association, the Palouse Prairie (*Agropyron-Festuca*) Association and the Fescue Prairie (*Festuca scabrella*) Association". The Fescue Prairie Association extends along the foothills in western Alberta in the Black soil zone and lies between the Mixed Prairie Association to the E and the "montane forest region" and the "aspen parkland region" (*Populus tremuloides*) to the W. Fescue Prairie has been discussed in detail by Moss (1944) and by Moss and Campbell (1947) and has been reviewed in relation to other Alberta vegetation types by Moss (1955).

The Dominant² species of the Fescue Prairie Association is *Festuca scabrella* (rough fescue) which forms large tussocks. This grass can grow almost to the exclusion of other vascular plants. However, as a result of mowing and grazing over much of the range of the Fescue Prairie Association, rough fescue has been replaced by such species as *Agropyron* spp., *Danthonia* spp., *Festuca idahoensis*, *Helictotrichon hookeri*, *Koeleria cristata*, *Poa* spp. and

² Those few species which provide most of the plant cover throughout a vegetation type, see page 102.

Stipa spp. (Moss and Campbell, 1947). The *Festuca-Danthonia* association of SW Alberta, as described by Moss (1944) is characterized by the co-Dominance of *Danthonia parryi* and *Festuca scabrella*. However, Moss and Campbell (1947) and Coupland (1961) have shown that *Danthonia* is co-Dominant only in grazed and mowed areas and that *Festuca scabrella* generally outranks all other species sufficiently to justify the term "Fescue Prairie Association", even for SW Alberta. The Fescue Prairie Association in the Alberta foothills alternates with extensive areas of aspen woodland, which are SW extensions of the aspen grove and parklands of central Alberta and Saskatchewan (Bird, 1961).

Küchler (1964) named the grassland in N central Montana that is continuous with the Fescue Prairie Association in SW Alberta, "Foothills Prairie" (*Agropyron-Festuca-Stipa*) and said it is characterized by the Dominance of *Agropyron spicatum*, *Festuca idahoensis*, *F. scabrella* and *Stipa comata*.

Moss (1955) showed that the *Agropyron-Festuca* zone, the most mesic of the three grassland zones described in southern British Columbia by Tisdale (1947) and included in the Palouse Prairie Association by Coupland (1961), has close affinities with the Fescue Prairie Association, especially that in SW Alberta. A brief description by McLean and Holland (1958) of the grasslands in the upper Columbia River valley across the Continental Divide from Banff, Jasper and Waterton Lakes National Parks indicates that these grasslands, too, have close affinities with the Fescue

Prairie in W Alberta.

Moss (1952) describes the grasslands of the Peace River area in NW Alberta, which are geographically the closest to Jasper Park, as an *Agropyron-Stipa-Carex* community. He suggests that this grassland is an edaphic climax due possibly to poorly drained or inadequately aerated soils. The *Agropyron-Stipa-Carex* grassland is very similar in composition to the Fescue Prairie of Central and W Alberta but lacks the major Dominant, *Festuca scabrella*. Most of the Dominants in the Peace River grasslands are grasses which are secondary in the Fescue Prairie, notably *Agropyron trachycaulum*, *Stipa spartea* var. *curtiseta* and *Koeleria cristata*.

OBJECTIVES OF STUDY

The purpose of the research reported in this thesis was to study the low-elevation grasslands in Banff, Jasper and Waterton Lakes National Parks, chiefly with regard to the following objectives.

1. To obtain accurate quantitative descriptions of their floristic compositions, plant populations, vegetation structures and physical habitats.
2. To determine, by means of correlations between vegetation and environment in selected areas, some of the main controlling factors operating on these grasslands.
3. To construct a phytosociological classification of the grasslands by using a combination of quantitative synthetic techniques.

4. To obtain some measure of the relative primary productivity of these grassland types.

5. To compare the grasslands with published descriptions of grasslands in adjoining regions.

This study was limited to grasslands meeting the following criteria.

1. Occurring at elevations in or below the montane zone, the upper elevational limits of which were considered to be approximately 4,500 ft in Jasper, 5,000 ft in Banff and 5,500 ft in Waterton Lakes National Parks.

2. Of "natural" or "permanent" status, at least in recent times, that is, not including grassed areas recently cleared for local development, power lines, ski runs, *etc..*

3. Not being obviously disturbed by the development of recreation areas, for example, campgrounds, golf courses.

4. Having grass-dominated vegetation of a type not usually found in extremely wet or sub-aquatic habitats such as sedge marshes and bogs.

This study was concerned mainly with detailed investigations of the primary producer levels of the ecosystems and did not involve detailed descriptions of climate, geology, or the animal populations of the areas.

The study was intended to form a contribution to the ungulate rangeland studies of the Canadian Wildlife Service and to the long-term, comprehensive ecological studies of the National Parks of Alberta being made by

the Plant Ecology Laboratory of the Department of Botany, University of Alberta.

DESCRIPTION OF STUDY AREAS

Geology

The Banff and Jasper National Park study areas (Figs. 1-4) are in the Front and Main Ranges of the Rocky Mountains which are separated by the Lewis Fault. This Fault runs from Waterton Park northwards to beyond Jasper townsite. It crosses the Bow River valley just east of the Sawback Range and thereafter lies about one range E of the Banff-Jasper highway.

The Front Ranges are complex, folded and faulted sheets of grey Paleozoic carbonates and shales and often have exposed Mesozoic shales, sandstones and carbonates in the valleys. The Main Range is more simple and massive than the Front Ranges and is composed of older and harder strata — mostly red, green and grey Precambrian and Cambrian sandstones, quartzites, shales and limestones.

Most of the valleys in Banff and Jasper Parks run NW-SE and follow the dips between the Ranges. Only a few of the larger rivers have cut through the Ranges to form large valleys, for example, the Bow River in Banff Park and the Athabasca River in Jasper Park.

Waterton Lakes Park (Figs. 1 and 5) lies entirely within or close to the Main Range of the Rocky Mountains;

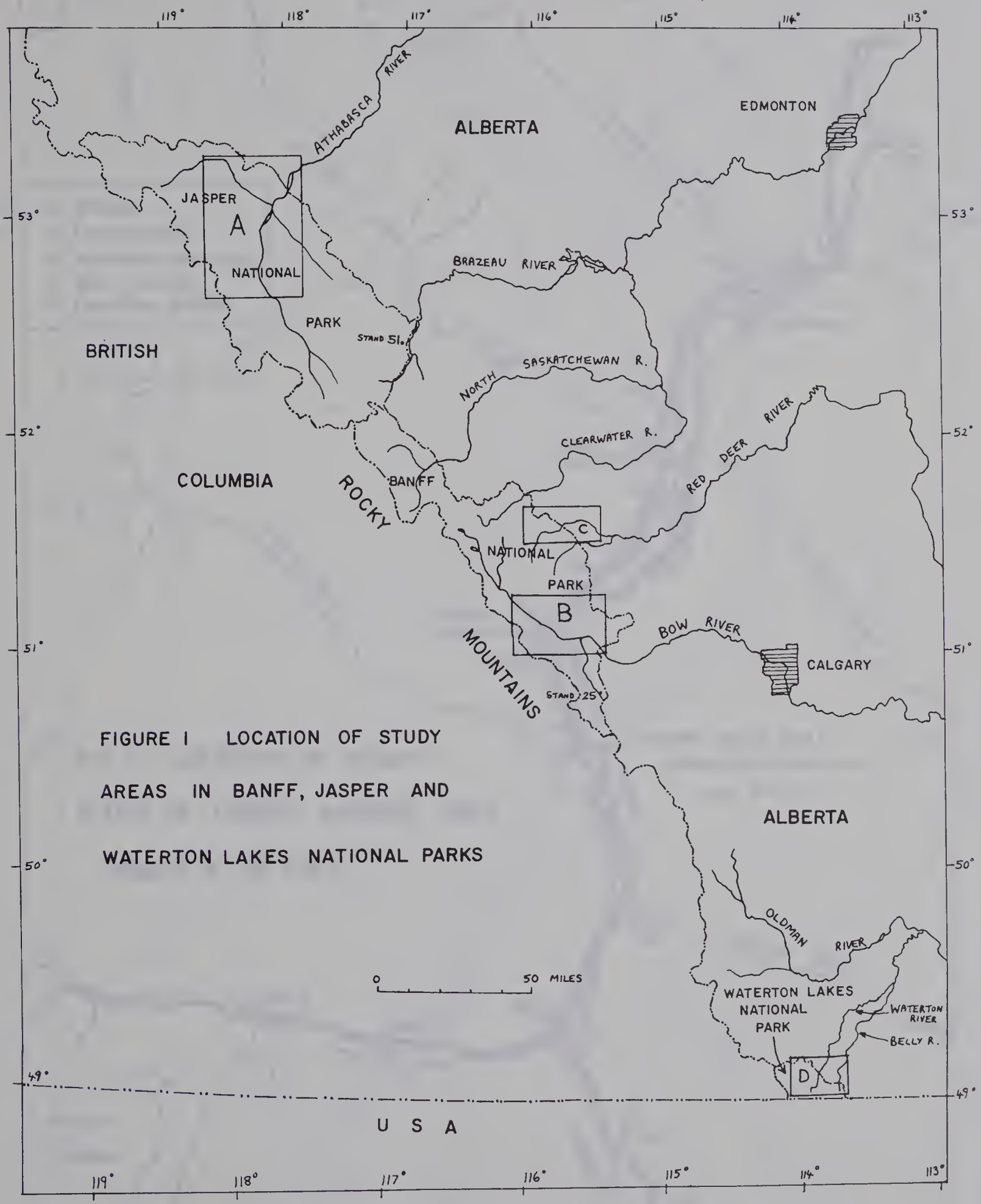
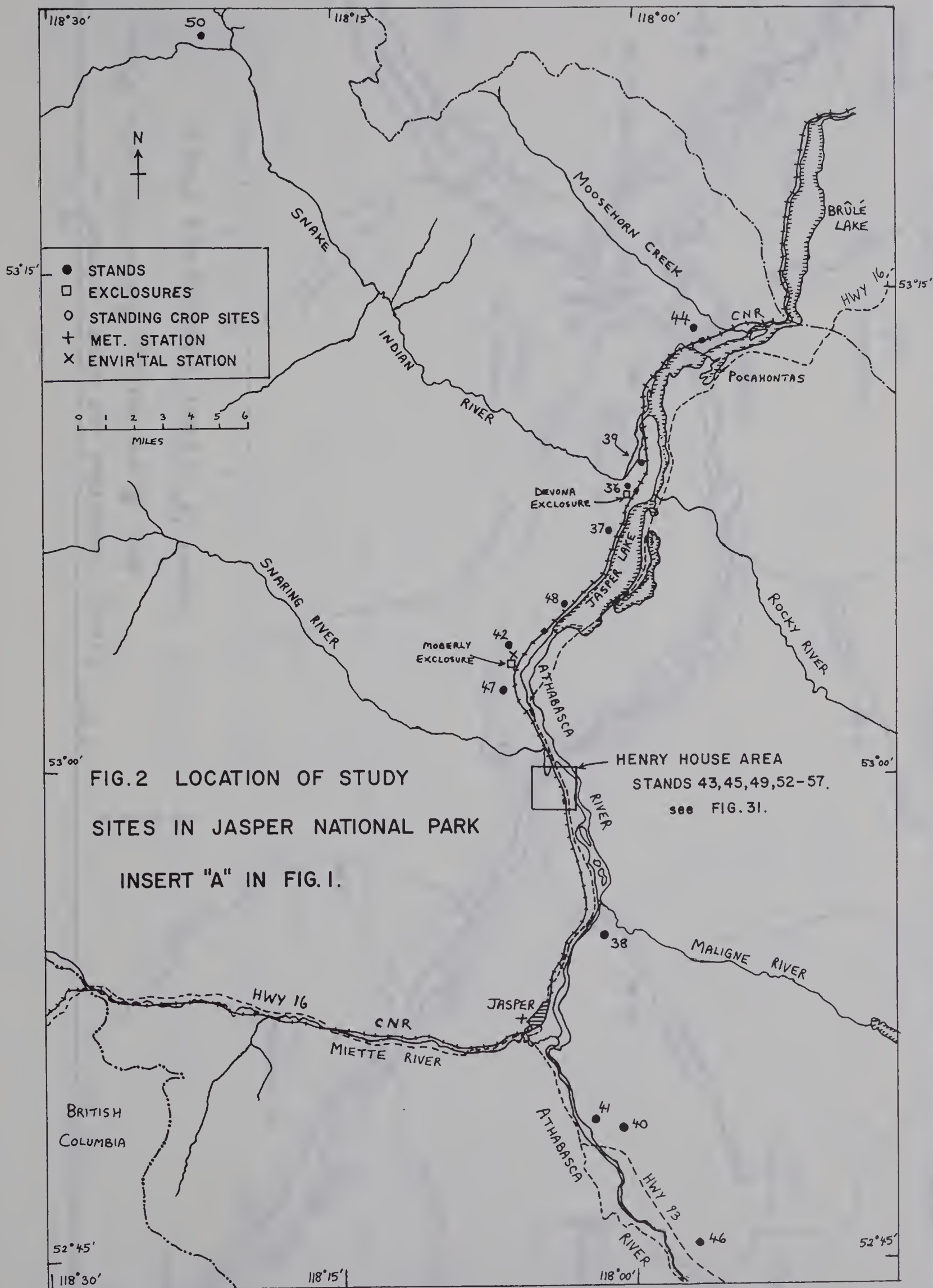


FIGURE 1 LOCATION OF STUDY
AREAS IN BANFF, JASPER AND
WATERTON LAKES NATIONAL PARKS



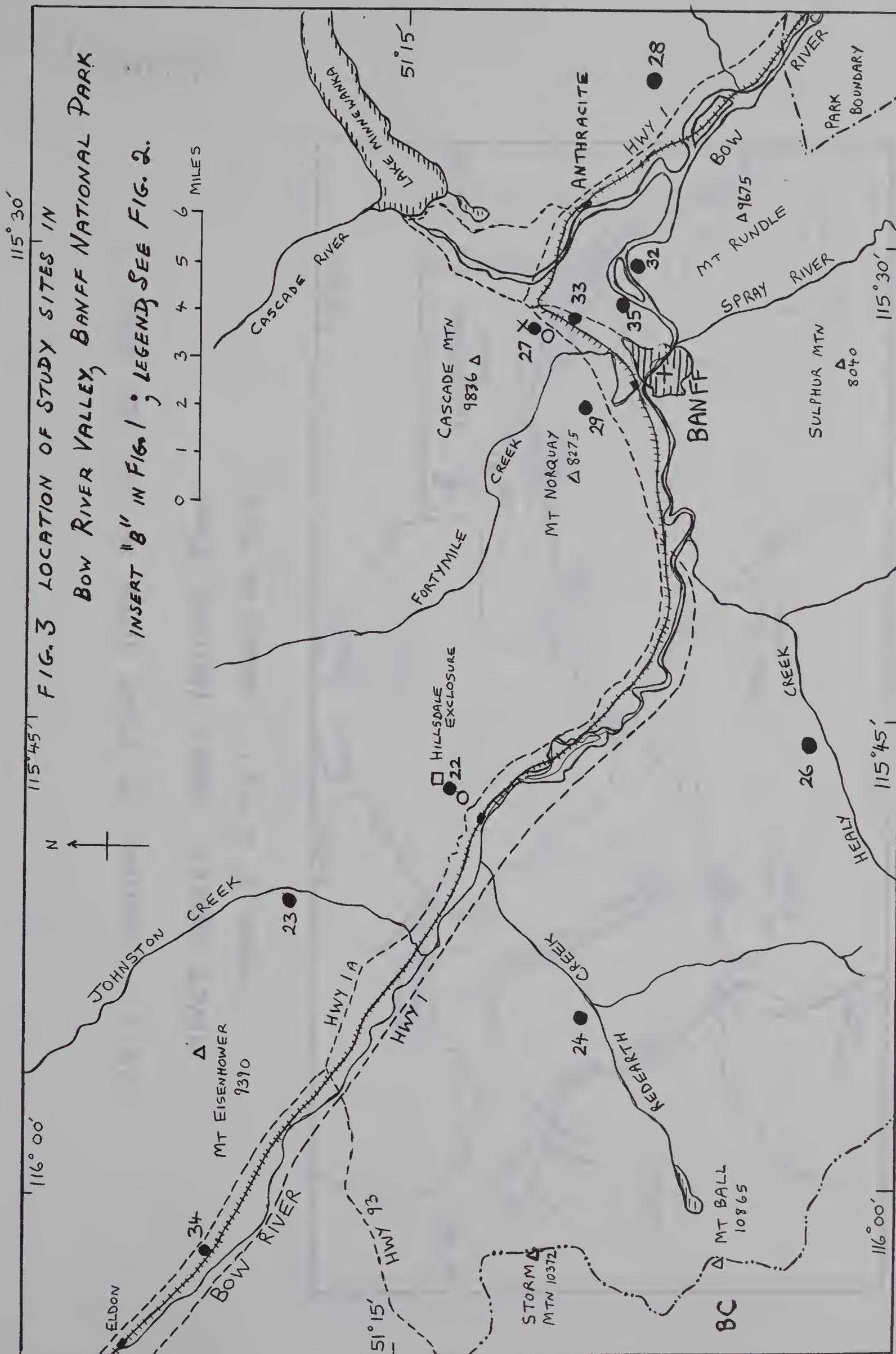
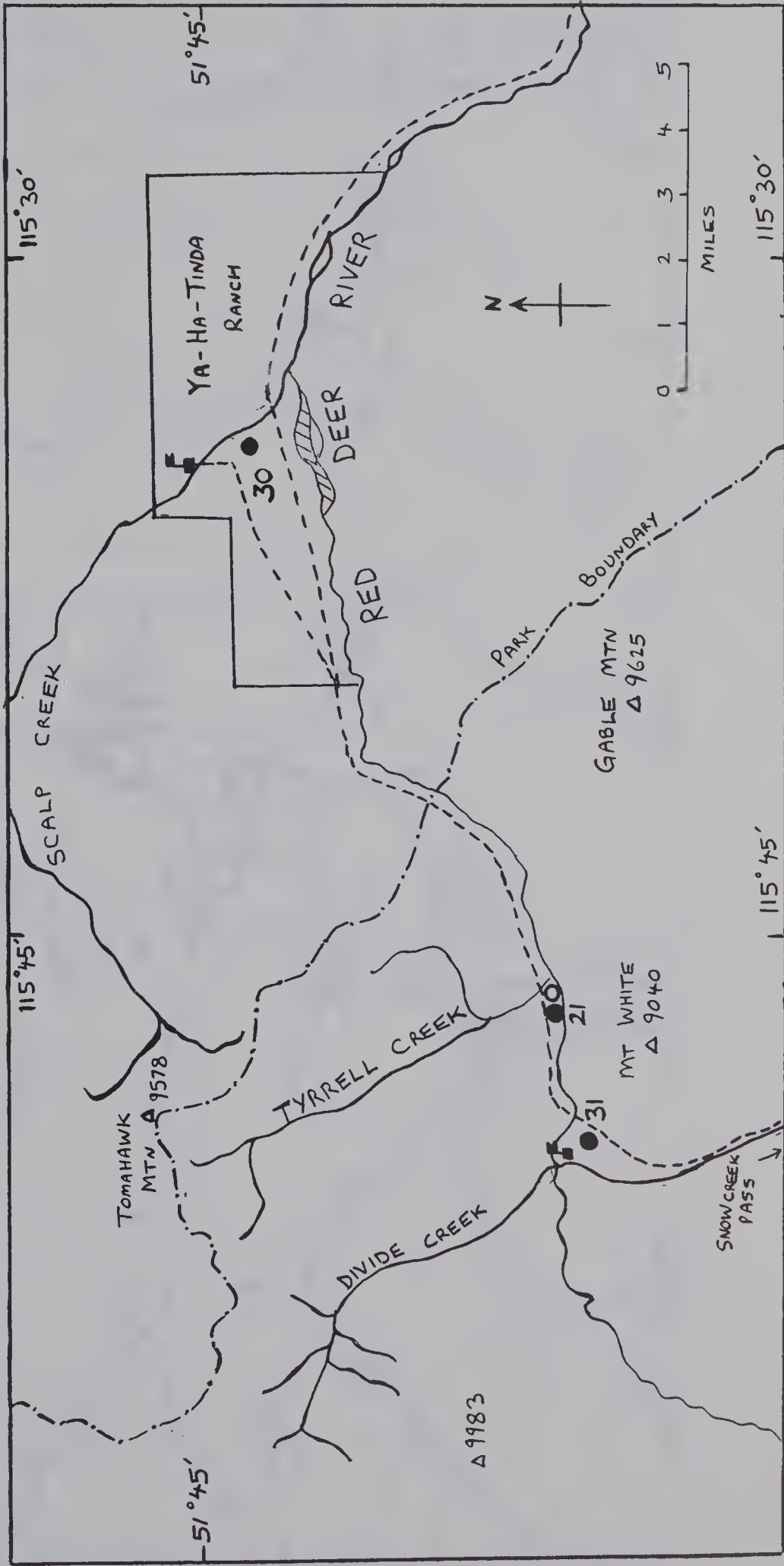
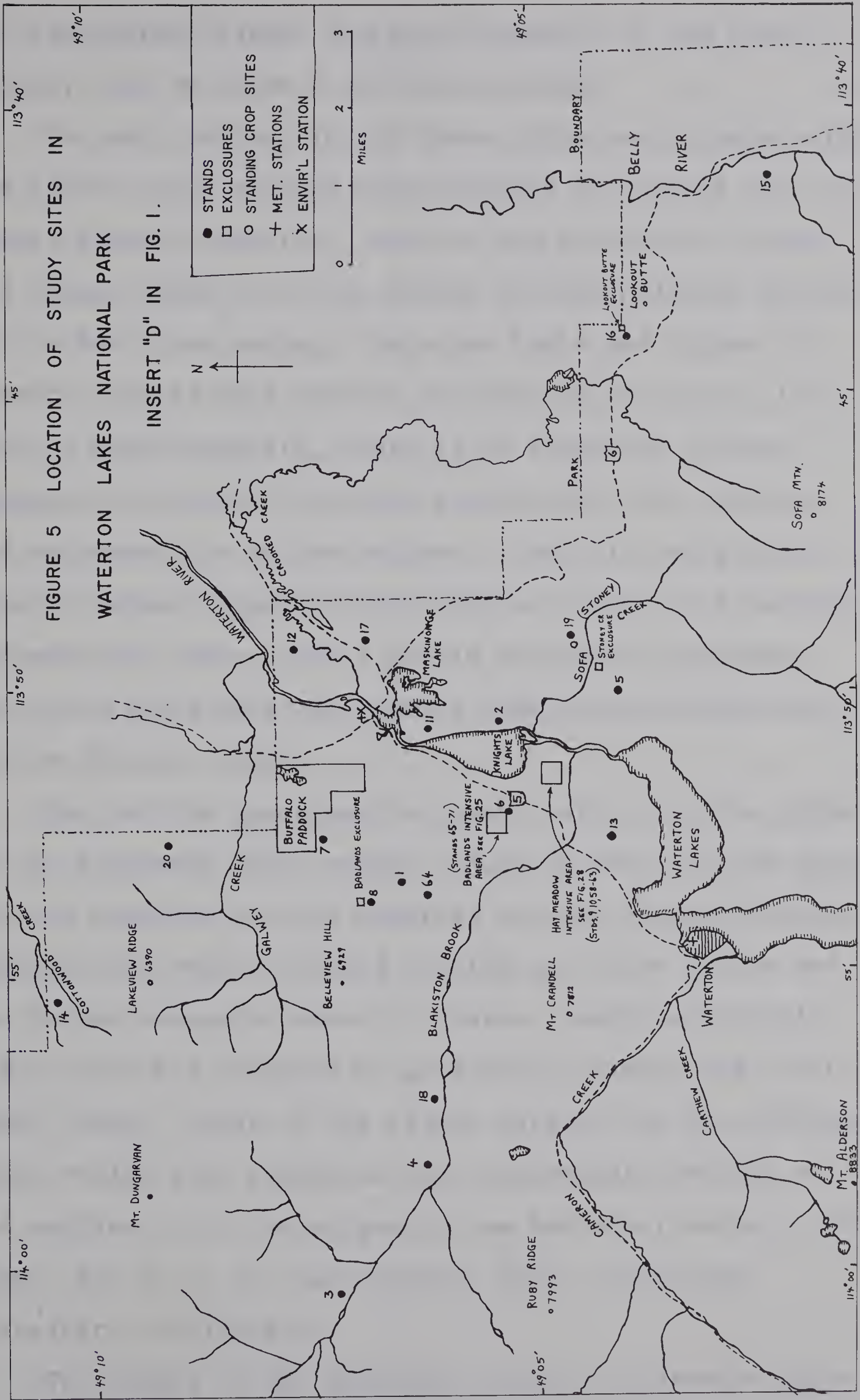


FIG. 4 LOCATION OF STUDY SITES IN THE RED DEER

RIVER VALLEY, BANFF NATIONAL PARK

INSERT "C" IN FIG. 1 ; LEGEND, SEE FIG. 2 .





the Livingstone Range, the most southerly of the Front Ranges, ends 50 miles N of Waterton Park.

The main valleys in all three Parks are U-shaped with the floors often covered with blankets of glacial till or glacio-fluvial deposits. Much of the grassland in Banff and Jasper Parks is on the plains of these glacial valleys. In the Bow River valley, there are knobs and ridges of bedrock covered with various thicknesses of glacial till. East of Banff townsite, there is an extensive terrace composed of outwash, probably formed after the glaciers had retreated far up the valleys. The till and glacio-fluvial outwash deposits are composed mainly of limestone, dolomite and shale, with a little quartzite sandstone, and are derived from the bedrock underlying the Bow River system (Rutter, 1965).

Most of the grassland in Jasper Park is on the plain of the Athabasca River valley. Much of the till and glacio-fluvial material and the material of post-glacial alluvial deposits has been re-worked by wind and water action and has formed extensive areas of coarse, sandy and gravelly flats which are occupied by grassland, savanna and coniferous forest. Many of the ridges parallel to the Athabasca River valley have sandstone and conglomerate bedrock at the surface (c.f. the ridges in the Bow River valley; pers. comm., Dr. H. A. K. Charlesworth, Dept. of Geology, University of Alberta).

The floors of the mountain valleys of Waterton Lakes

National Park are covered with post-glacial fan and alluvial deposits and generally have no glacial till (Horberg, 1954). One of these valleys, Blakiston Brook, has some grassland. However, most of the grassland in this Park is in the N-central part which is composed of rolling foothills traversed by the wide valley of the Waterton River. A large part of the foothills area flanks the Waterton River valley and is formed of ground moraine of both continental and mountain origin, for example, the "Badlands". There are eskerine complexes and a series of drumlins parallel to the valley (Horberg, 1954). There are other extensive grassland areas on the large, gravelly alluvial fans of Blakiston Brook and Sofa Creek in the mountain section of the Waterton River valley and of the North Fork of the Belly River valley. The glacial till and gravel are derived from local bedrock and are composed of Precambrian dolomites, limestones, argillites and quartzites and of Cretaceous sandstones and shales. There is a marked variability in composition of till and gravel over relatively short distances.

Climate

Alberta has a continental climate with cold winters and short, cool summers, primarily because of the Rocky Mountains' barrier to maritime influences. The prevailing winds are from the W, SW or NW (Longley, 1967).

The climates in the mountain valleys on the eastern slopes of the Rocky Mountains are transitional between three of the six types of climate of Canada designated according to region (Canada Department of Transport, 1962); the Prairie, Cordillera and Northern Climatic Regions.

Climatic data (D.O.T. Meteorological Stations) for the Alberta Rockies, although scant, are mostly from the bottoms of the main valleys, where the study areas are located. Climatic conditions in these valleys are much different from those elsewhere in the mountains because of the effects of altitude on temperature and precipitation, and because of cold air drainage and valley winds, *etc.* These mountain valleys are affected more by maritime influences than are other regions of Alberta, and their winter temperatures are generally higher than those in other parts of the Province at the same latitude. In summer, temperatures in these valleys are often lower than those on the plains, mainly because of higher altitude.

Summaries of the temperature and precipitation records from four meteorological stations within the study

areas are given in Tables 1 and 2 and Fig. 6. These data were obtained from the Climatology Division of the Meteorological Branch, Department of Transport, Toronto (Anon., 1964, 1965).

Figs. 2, 4 and 5 (p. 9, 11 and 12) show the positions of these weather stations in relation to the locations of the stands studied.

Since most of the grassland sites are on slopes at the bases of mountains or in valley bottoms, the elevations of the weather stations are roughly the same as those of the stands.

The climates at the stations at Banff and Jasper townsites and at Anthracite (within the Banff study area) are similar and differ only as follows: Jasper has slightly warmer summers than Banff but slightly colder winters. The mean annual temperature at Jasper is 1.3 F higher than that at Banff and 0.5 F higher than that at Anthracite. At all three stations, the coldest month is January and the warmest month July.

Although the total rainfall is similar for the three stations, Jasper has the lowest annual snowfall (about 30 inches less than Banff and 15 inches less than Anthracite). Therefore, the total annual precipitation is about 16 inches at Jasper (about 2.5 inches less than that at Banff or at Anthracite).

At all three stations, the highest rainfall is usually in June, averages being 2.15 inches at Jasper, 2.41 inches

TABLE 1. TEMPERATURES AT FOUR METEOROLOGICAL STATIONS IN THE STUDY REGION

Expressed as normals for period of 30 years (1931-60) in ° Fahrenheit (Anon, 1964).

Station, Location and Elevation in Feet	Mean Annual	Hottest Month ^a			Coldest Month ^a		
		Mean Daily	Mean Daily Maximum	Mean Daily Minimum	Mean Daily	Mean Daily Maximum	Mean Daily Minimum
Anthracite 4500 51°53'N, 115°29'W	36.8	58.6	73.5	43.7	13.4	22.4	4.4
Banff 4538 51°11'N, 115°34'W	36.0	58.0	72.5	43.5	12.6	21.7	3.5
Jasper 3472 52°53'N, 118°04'W	37.3	59.4	73.6	45.2	11.5	21.0	2.0
Waterton Park HQ ^b 4250, 49°4'N, 113°57'W	40.9	63.2	75.1	51.2	18.5	27.0	9.9

NOTES: ^a For all four stations the hottest month is July
^b For all four stations the coldest month is January

^b Based on a period of less than 10 years, but adjustments have been made when an unusually warm or cold month unduly influenced the average values.

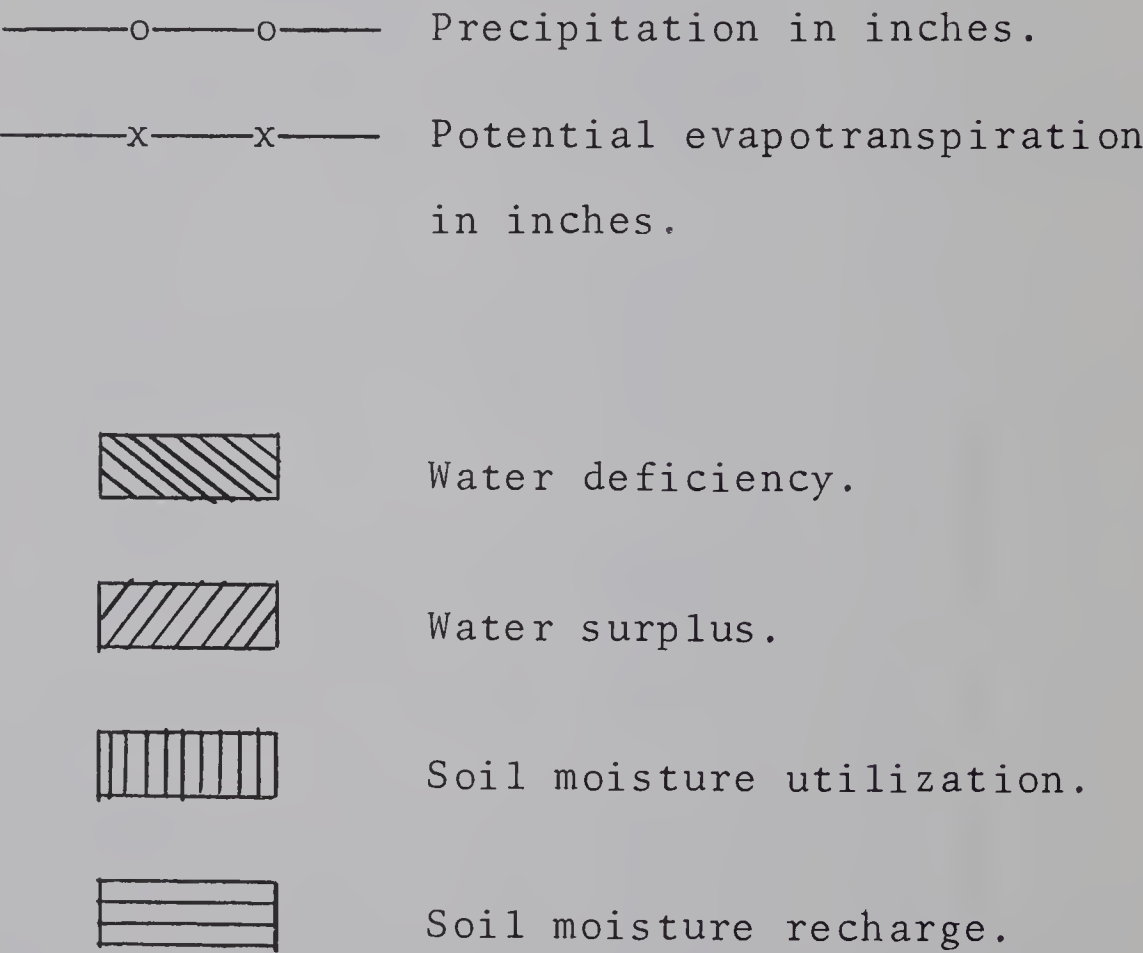
TABLE 2. PRECIPITATION AT FOUR METEOROLOGICAL STATIONS IN THE STUDY REGION
Expressed as normals for period of 30 years (1931-60) in inches (Anon, 1965).

Station	Annual Precipitation	Annual Rainfall	Annual Snowfall	Highest		Highest Monthly Precipitation
				Monthly Rainfall	Monthly Snowfall	
Anthracite ^b	18.34	11.91	64.3	2.65 June	11.6 Jan.	2.68 June
Banff town	18.48	10.55	79.3	2.41 June	14.0 Dec.	2.45 June
Jasper town	15.98	11.06	49.2	2.15 June	10.9 Dec.	2.15 June
Waterton Park HQ ^a	42.31	19.46	228.5	4.99 June	38.0 Jan.	5.17 June

NOTES: ^a Based on a period of record of 10-24 years during 1931-60

^b 3 mls east of Banff townsite.

Figure 6. Climatic diagrams for meteorological stations within Banff, Jasper and Waterton Lakes National Parks.

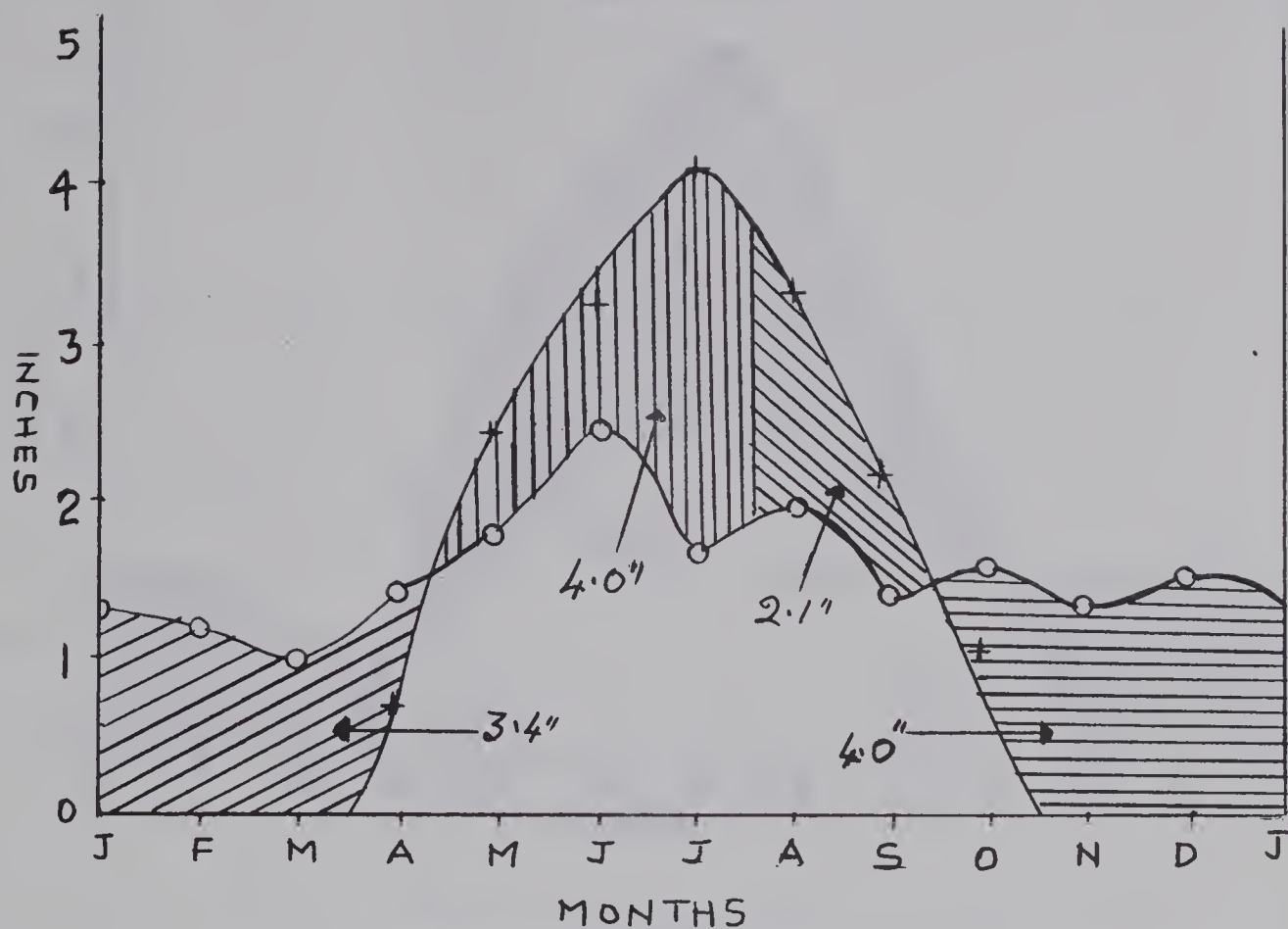


- A. Banff.
- B. Anthracite.
- C. Jasper.
- D. Waterton Park H.Q.

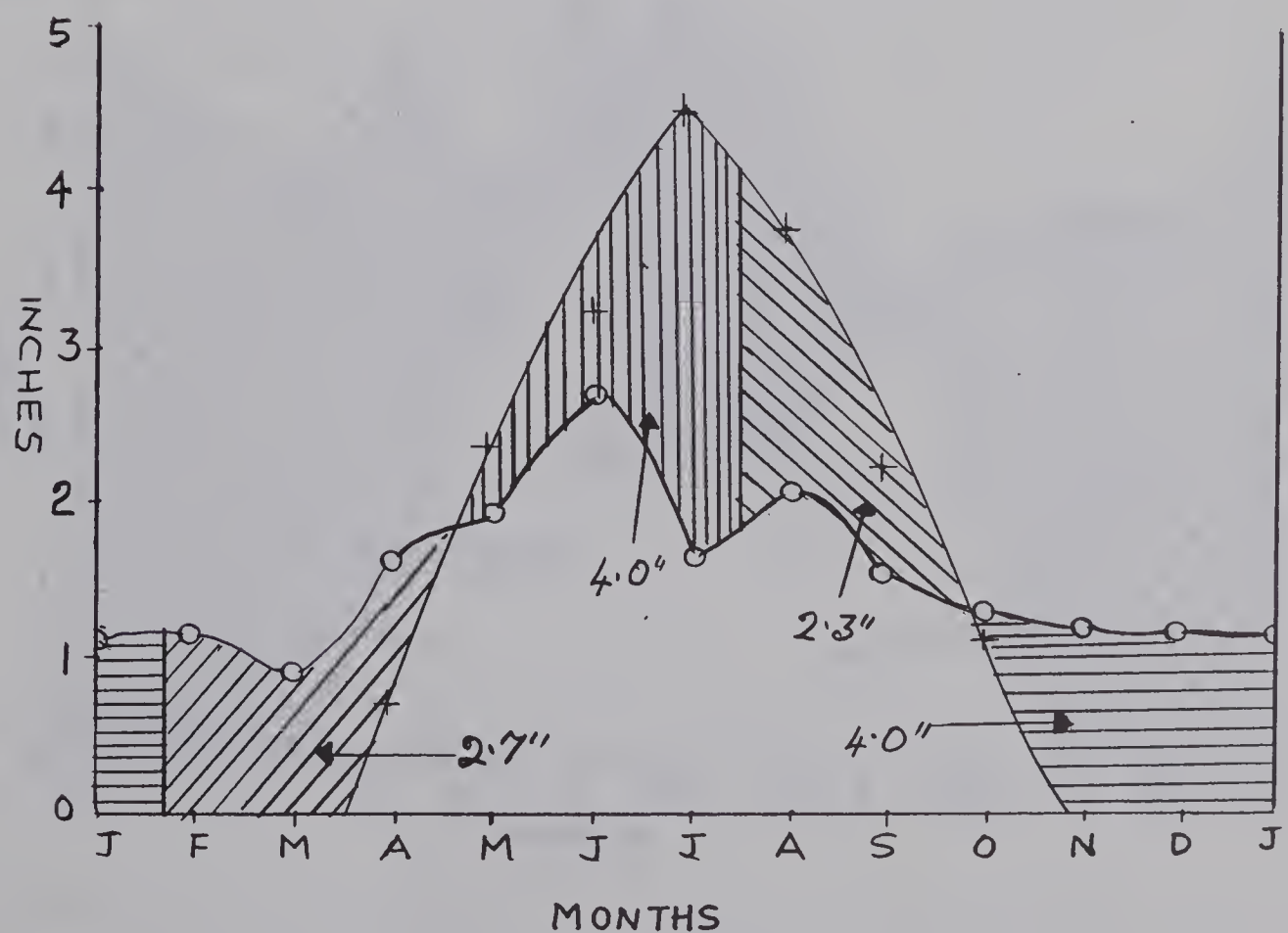
FIGURE 6

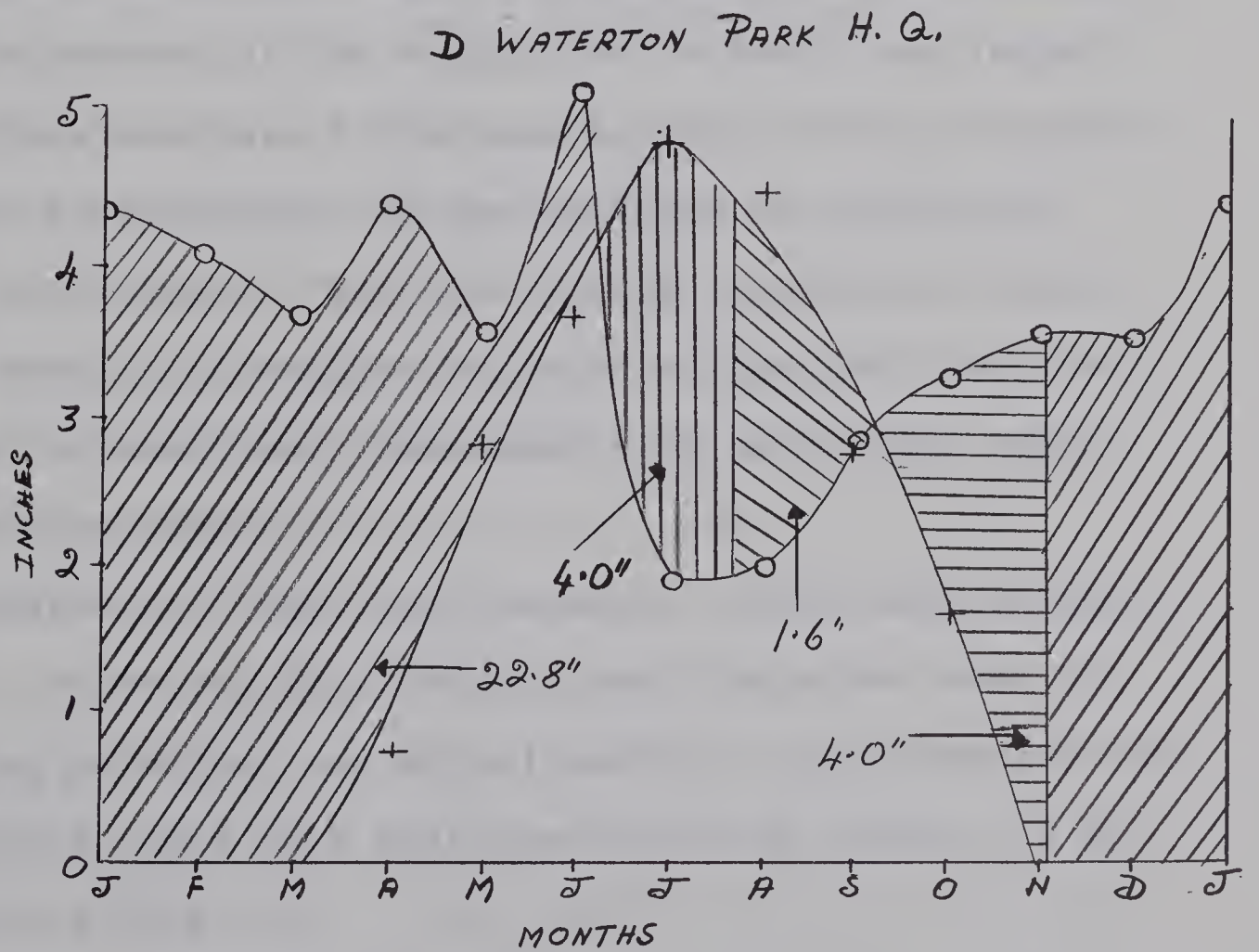
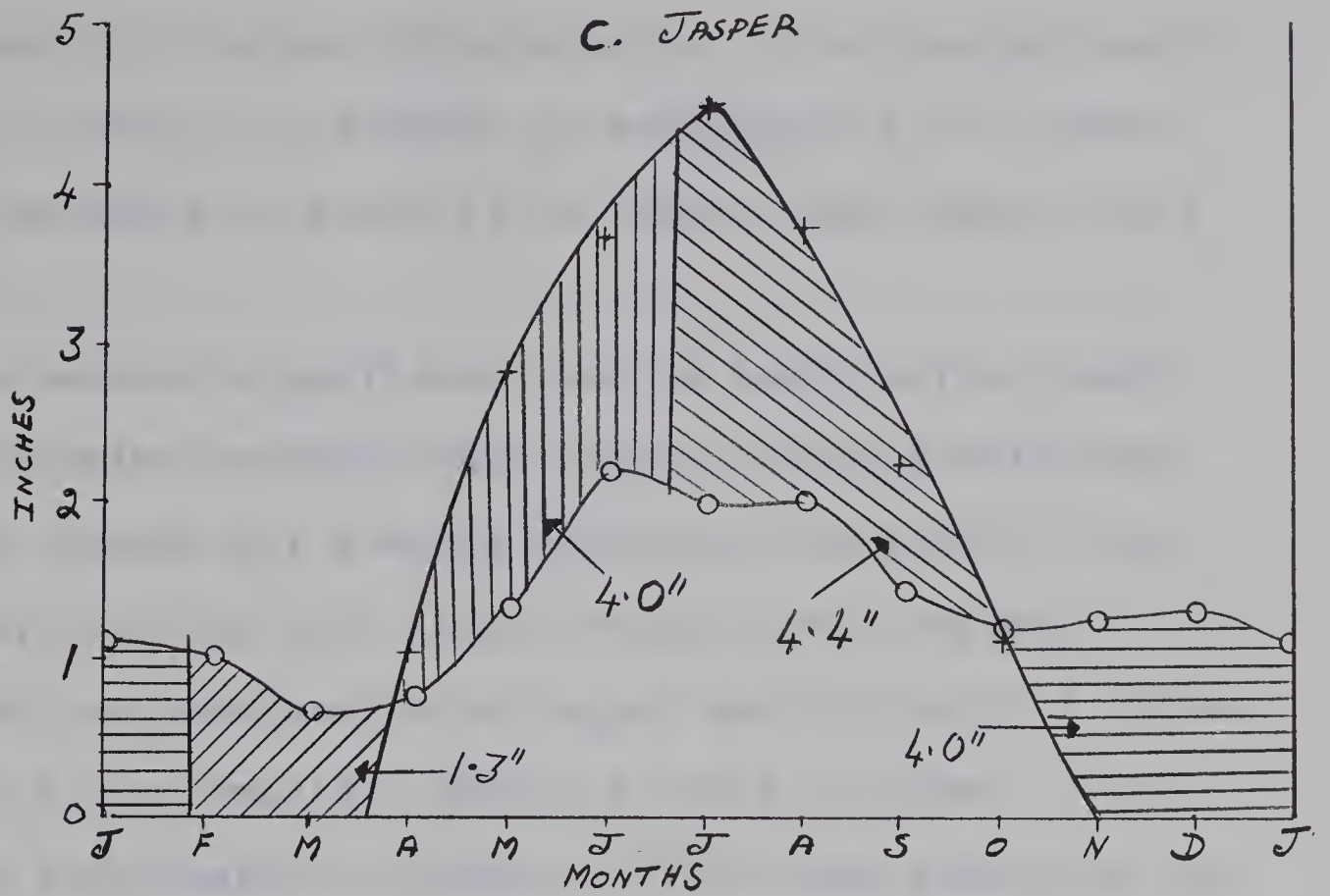
A BANFF

19



B ANTHRACITE





at Banff and 2.65 inches at Anthracite. The heaviest monthly snowfall is usually in January at Anthracite (11.6 inches) but is in December at Banff (14.0 inches) and Jasper (10.9 inches).

It is perhaps significant that in early spring Banff often has heavier snowfall than Jasper. During March and April, the figures for average precipitation (mostly snow) at Banff are 8.9 and 10.0 inches respectively whereas figures for the same months at Jasper are 5.0 and 2.7 inches. Anthracite is intermediate with 8.0 and 5.9 inches. This results in differences in amounts of moisture available for spring growth and could lead to differences in the composition and structure of the vegetation in Banff and Jasper. However, this moisture difference may not be very significant since precipitation in May and June is relatively heavy in both areas. The lower spring snowfall at Jasper probably results in earlier exposure of the soil surface there than at Banff and consequently in an earlier onset of the growing season.

An analysis of the water balances of the main valleys of Banff, Jasper and Waterton National Parks was made by calculating potential and actual monthly evapotranspirations and comparing these data with precipitation normals at the four stations (Fig. 6).

Evapotranspiration was calculated by the method of Thornthwaite (Thornthwaite and Mather, 1957) based on the monthly mean temperature and station latitude. Since there

was no more accurate estimate available, a soil moisture reserve of 4.0 inches was used, as recommended by Thornthwaite and Mather (1957) for sandy "pasture" soils and by Sanderson (1948) for most agricultural soils. This soil moisture reserve varies according to the type of vegetation and to the texture and depth of the soil so that quite small variations in topography, soil or vegetation result in changes in soil moisture reserve values.

Potential evapotranspiration at Jasper is much greater than precipitation in spring and early summer. Therefore, reserve moisture in soils at Jasper is exhausted earlier than in soils at Banff or Anthracite. Jasper has a three-month period of soil moisture deficiency in summer whereas Banff and Anthracite deficits last about two months.

These moisture deficits may shorten the "Effective Growing Season" which has been defined on temperature criteria alone as the number of days with mean temperatures above 42 F, discounting those individual warm days outside the normal growing season (Boughner, 1964). The Effective Growing Season at Jasper is nine days longer and begins four days earlier than at Banff (Boughner, 1964). It is probable that higher elevation and the heavier snowfall in winter and especially in early spring result in a later onset of the Effective Growing Season at Banff. However, it is also probable that the Effective Growing Season at Jasper is terminated by soil moisture deficits earlier than that at Banff, so that the period over which most

plant growth occurs may be about the same length in both areas.

The differences in climate between Banff, Anthracite and Jasper are much less striking than the differences between their climates and that at Waterton. Waterton has much warmer summers and winters (Table 1) and much higher rainfall in summer and snowfall in winter (Table 2). Unfortunately, no data are available on the Effective Growing Season, but the climate of Waterton appears to be more moist and temperate than that of Banff or Jasper. The late summer period of moisture deficiency is only about one month long because of the heavy precipitation which exceeds potential evapotranspiration right up to the end of June (Fig. 6). The late summer moisture deficiency of 1.6 inches is soon replenished in the fall, and a moisture surplus of 22.8 inches accumulates as snow during the rest of the winter. The precipitation more than compensates for the higher evapotranspiration and results in much more mesic environmental conditions at Waterton.

Soils

At present, there is no published description of the soils of Banff, Jasper and Waterton Lakes National Parks. The few existing descriptions of soils within Alberta's Rocky Mountains or foothills were not considered directly applicable to this study.

Fire History

The Banff, Jasper and Waterton Lakes areas were established as National Parks in 1885, 1907 and 1911 respectively. Waterton Lakes was established as Kootenay Lakes Forest Reserve in 1895. As fire records were kept only after the Parks had been in existence as such for a few years, the history of fires in these areas before these dates is scanty. However, it is evident that, before records were kept, fires were widespread and frequent, especially in the main valleys, where the study areas are located. Very large areas of even-sized and probably even-aged lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.) indicate the extent, effects and dates of these fires in Banff and Jasper National Parks. The fires were often begun by lightning, Indians or early explorers. There are reports that prospectors lit many fires to aid in uncovering rock strata and to mark areas for further digging.

Fires begun by sparks from steam locomotives were very common during and for some time after the years of railroad construction in Banff (1883-5). Tracks were laid in Jasper Park in the years 1910-12 and an increase in fire frequency there may also have occurred then. As no railroad has been constructed through Waterton Lakes National Park, this area did not have the wide-spread fires associated with railroad construction. The Waterton Park Superintendent's report for 1915 states that "there was no trouble with fire during the year, due largely to the fact

that no railroad touches or traverses the park".

For the past fifty years, fires in the three Parks have been frequent but small and have been mainly in grassland, scrub or forest litter close to areas of human activity in the main valleys. The frequent occurrence of small ground fires could, over a number of years, maintain small areas of grassland in the main valleys in Banff and Jasper National Parks on sites where forest would normally exist. Thus, it may be significant that many of the small areas of grassland at elevations where there is usually coniferous forest are close to railroad tracks or townsites.

It is also probable that grassland is maintained over forest in transitional areas by the grazing and browsing of native ungulates and horses. Thus, two partially conflicting factors may be acting at present: (1) the Parks' fire control policy which should result in increasing the area of mature, climax forest at the expense of fire-maintained grasslands and scrub, and (2) the maintenance of grassland and scrub through frequent disturbance by man and ungulates.

Grazing History

The four important native ungulates in the lower valleys of Banff, Jasper and Waterton Lakes National Parks are the bighorn sheep (*Ovis canadensis canadensis* Shaw), mule deer (*Odocoileus hemionus hemionus* (Rafinesque)), moose (*Alces alces andersoni* Peterson) and elk (*Cervus*

canadensis nelsoni Bailey).

Mule deer and moose feed mainly on leaves and shoots from shrubs and young trees. Bighorn sheep are grazing animals and feed on grasses and forbs. Elk feed on grasses, shrubs or herbs. Before 1880, elk were abundant in the Rocky Mountains but, except for one small herd in Jasper Park, they disappeared from the Alberta Rockies during the 1880s, probably because of severe winters (Flook, 1964) and increased hunting, mainly by Indians after the disappearance of the buffalo.

When Banff and Jasper National Parks were established, mule deer, moose and bighorn sheep were more numerous in the Park areas than elk. Elk from Yellowstone National Park were released in both Parks between 1918 and 1920 and animals also migrated over the Divide from British Columbia.

The grazing and browsing ranges of the ungulates have been increased by the large areas of successional grassland and scrub vegetation in Banff and Jasper Parks. These areas have resulted from the widespread and largely unchecked fires taking place before the introduction of the fire control policy.

The combined effects of fire-control, hunting-prohibition and predator-eradication policies have permitted a steady increase in the populations of all four ungulates. By the 1940s, range conditions became critical in Banff and Jasper Parks, especially in the low-elevation,

light-snowfall areas used by bighorn sheep, mule deer and elk as winter grazing grounds (Flook, 1964). Elk reached population peaks in Banff and Jasper Parks in the early 1940s, when range depletion was recognized and herd reductions begun. Since then, the numbers of elk have been held in check by annual harvests of up to 700 in Jasper and 400 in Banff Park in the 1940s and smaller numbers since.

In winter, bighorn sheep graze mainly on graminoid species and are usually on grassy, S-facing slopes and ridge tops, where snow cover is minimal. In summer, they also feed on forbs, especially legumes such as *Astragalus* spp., *Hedysarum mackenzii* and *Oxytropis* spp. (Flook, 1964).

Mule deer browse on such preferred species as *Amelanchier alnifolia*, *Populus tremuloides*, *Salix* spp. and *Cornus stolonifera* (Shepherd, 1960). Large numbers of deer remain in the valley bottoms throughout the year and frequent shrubby areas and forest edges. They avoid deep snow in winter. In some areas where the preferred browse species have been depleted by elk, they feed on species of low palatability, such as *Arctostaphylos uva-ursi*, *Juniperus horizontalis*, *Shepherdia canadensis* and *Pseudotsuga menziesii* (Cowan, 1947).

Moose also browse throughout the year on preferred species similar to those of mule deer. However, a large part of their summer diet consists of aquatic plants (Flook, 1964). Moose can tolerate greater snow depth than mule deer or bighorn sheep. They inhabit moist, shrubby meadows

throughout the year and stay especially near streams and shallow lakes in summer.

Since elk have very adaptable feeding habits, they are found in a wide variety of habitats. In Banff and Jasper Parks, their present diet consists mainly of graminoid species, and shrub species are of secondary importance in summer and of very minor importance in winter. Since aspen and other preferred browse species were depleted by the large populations of elk in the 1930s and 1940s, elk now browse on species of lower palatability, such as *Shepherdia canadensis* and *Arctostaphylos uva-ursi*. Stands of aspen have not recovered and areas killed by bark-stripping have little apparent regeneration (Flook, 1964).

Flook (1964) reported that in Banff and Jasper Parks elk and bighorn sheep populations were large, moose smaller and mule deer smallest.

The first authentic record of an elk in Waterton Lakes National Park was in 1920. Migration from Glacier National Park and the Flathead Lake and Valley areas in Montana increased the numbers of elk considerably. In 1945, Cowan estimated their number at about 500, and in 1967 surveys by the Canadian Wildlife Service showed that this number had increased to about 700. Their winter feeding ranges, which include prairie, aspen parkland and some mixed forest areas, are in the open or semi-open eastern foothills areas of the Park. Their summer ranges are at much higher elevations in the subalpine and alpine zones.

The population of mule deer in Waterton Lakes Park has been large for at least the past fifty years. Banfield (1947) estimated the number at 1,700. Since elk numbers increased in the Park in the 1930s, mule deer numbers decreased, falling to about 400 by 1967. Mule deer range over the whole Park but are especially frequent in the aspen parkland-grassland transition areas.

As white-tailed deer (*Odocoileus virginianus dacotensis* Goldman and Kellogg) seem to be better adapted to living near human settlements, they have been replacing mule deer in much of the aspen parkland in western Canada (Bird, 1961). However, they have been described as "occasional visitors only" in Waterton Lakes Park (Banfield, 1947), and observations since 1947 show that the population is fairly stable at 12-28 animals. They are found in the low-lying aspen woodlands on the E side of the Park.

Bighorn sheep in Waterton Lakes Park feed in the alpine and subalpine areas in summer and either move down to the montane zone in winter or stay at high elevations on exposed, snow-free ridges. They are rarely seen in the low-elevation grassland areas except for a small herd which frequents the townsite area. Their total number in the Park in 1967 was estimated at 321-377 (Stelfox, 1967).

Before Waterton Lakes was established as a National Park, the grasslands there were open range and public grazing lands.

The Park Superintendent's report for 1910-1911 states

that "there are about 15 square miles of grazing land" and "during last winter (1910-1911) there were over 15,000 cattle and 100 horses which drifted up here for shelter" and "they eat all the hay and feed there is". Although, after 1915, grazing was by permit only, there were still 2,900 head of domestic livestock in the Park in 1919. As the summer was very dry and the grazing excessive in 1919, grazing of only cattle and horses was allowed and domestic sheep were excluded. Grazing of domestic livestock was not prohibited until 1947. Private saddle-horses and saddle-horse concessions were still permitted. The former horses have, since 1947, been allowed to graze in special communal pastures within the Park, while horses from the concession stables may graze on a 4 square mile area of fescue prairie on the Badlands.

In all three Parks, the introduction of horses may have had a considerable effect on the grasslands. In pastures, horses spread many seeds via their droppings, whereas cattle, sheep, elk and deer chew their cud and destroy most of the seeds they consume (Bird, 1961).

In 1917, 20 acres in the Dardanelles area of Waterton Lakes Park were ploughed and sown with oats and timothy grass. In subsequent years this seeded area was increased, reaching 200 acres in 1924. Since 1917, large areas of meadows suitable for hay production have been added and are harvested at yearly or two-yearly intervals for timothy, brome and rye grass hay. In 1966, 146 tons of hay were harvested, 75 tons of which went to Banff National Park.

METHODS

Stand Selection

As a necessary initial step, aerial photographs and topographic maps were studied to find all grassland sites in relatively low-lying areas in the three Parks. No attempt was made to evaluate critically the zonal relationships of these grasslands. An upper altitudinal limit for areas to be considered was set in each Park, approximating to the upper limit of montane forest. By referring to elevational data on Douglas fir (Stringer, 1966) and making latitudinal-elevational adjustments, this limit was estimated very approximately to be at about 4,500 ft in Jasper National Park, 5,000 ft in Banff National Park and 5,500 ft in Waterton Lakes National Park.

Knowledge acquired during earlier ecological studies in some of these areas (Stringer, 1966) was useful in distinguishing grassland from other vegetation types and it was possible to detect grassland sites with reasonable accuracy. Confusion between grassland and sedge marsh sometimes occurred, but studies of topography, together with the darker tone of wetter areas on aerial photographs, usually enabled a correct identification to be made. However, this method of selection probably resulted in the exclusion of some moist grassland sites thought to be marsh.

During the summer of 1967, an attempt was made to

sample all grassland sites considered large enough (more than $60,000 \text{ ft}^2 = 5,574 \text{ m}^2$) to merit further study. A list of aerial photographs with sampling areas is in Appendix 2, p. 314.

Grasslands were so extensive in Waterton Lakes and Jasper National Parks that there was considerable choice of sampling locations in both Parks, although grassland was far more extensive in the former than the latter. On the other hand, Banff National Park, owing to the higher elevations of its main valleys, contained no large grassland areas, the only grass areas being isolated and comparatively small.

Owing to the author's initial lack of knowledge of disturbance due to man, little attempt was made to include only "natural" areas. However, the following criteria of stand selection were adhered to.

1. Each stand had to have a reasonably uniform topography, thus ensuring as few major environmental discontinuities as possible.
2. Severely disturbed areas with obviously artificial grasslands were avoided. These included golf courses, campgrounds, disturbed roadside clearings, *etc.*
3. The vegetation cover of each stand had to be composed predominantly of grasses, with trees or large shrubs of only isolated occurrence. Areas of permanently or semi-permanently

saturated ground, such as sedge marshes, were omitted.

By applying these criteria, a wide variety of grassland types could be sampled, ranging from very xeric, overgrazed areas to moist, low-lying meadows.

Extensive Sampling Scheme

1. Vegetation

Between June 13 and August 31, 1967, 51 "stands" were studied, each stand being 200 ft by 300 ft (61 m x 91 m) (Appendix 1, p. 312, Figs. 1 - 5, p. 8 - 12). The sampling method at each site was as follows.

The population size of each shrub, herb, bryophyte and lichen species was subjectively estimated by means of a modified Braun-Blanquet (1932) Cover-abundance scale as follows:

P--Rare

+--Common, but cover less than 1%

1--Abundant, with cover between 1% and 5%

2--Abundant, with cover between 5% and 15%

3--Abundant, with cover between 15% and 25%

4--Abundant, with cover between 25% and 50%

5--Abundant, with cover between 50% and 75%

6--Abundant, with cover between 75% and 100%

In preference to assigning a Cover-abundance value to each species in the stand area by simple, gross inspection, it was decided to subsample the area with 2 m x 2 m quadrats, and then to arrive at a more accurate value by

averaging the estimates from the subsamples. A restricted random sampling method was used whereby the stand was divided into six 100 ft x 100 ft blocks. The quadrats were placed at random loci in each block by using a random numbers table. The sequence of area sampling was also random. The following observations were made in each quadrat:

1. A complete list of vascular plant, bryophyte and lichen species present. Each species was assigned a Cover-abundance value.
2. Slope angle across the quadrat centre with an Abney level.
3. Slope aspect, with a Silva Ranger pocket compass.
4. Soil temperatures at a depth of 15 cm at the quadrat centre, with a 20 cm Weston dial probe thermometer.
5. Air temperatures at a height of 4 ft, with a shielded alcohol-in-glass thermometer.

Quadrats were sequentially sampled until a previously-fixed, minimum standard error, set at 15% of the mean Cover-abundance value of the most important species was obtained. It was soon found that sampling 10 quadrats in uniform grassland was usually more than sufficient to reach the required sampling efficiency. It was subsequently realised that a mean Cover-abundance value lacked validity because of the unequal cover ranges represented by the values. Therefore, the midpoints (%) of the cover ranges of each Cover-abundance value were used instead of the

scale values themselves, and the sampling efficiencies were recalculated for the number of quadrats sampled (usually 10). The recalculated values were about 10% higher than the original sampling efficiencies. This gave a standard error of 25% of the mean cover of the most important species.

The mean quadrat cover percentage of each species was calculated and used as guide to set a Cover-abundance value for that species, in the stand as a whole. For the less common species, including those not present in any of the quadrats, simple, gross inspection was resorted to. Each species was also assigned stand values for Sociability and Periodicity, according to the following scales (Braun-Blanquet, 1932).

Sociability

- 1--growing as single, distinct individuals
- 2--growing in small groups or tufts
- 3--growing in patches or small cushions
- 4--growing in intensive patches or forming extensive carpets
- 5--growing in extensive masses, and as pure stands of wide extent

Periodicity

- Fol--in foliage only
- F1 - flowering
- Fr - fruiting
- B - flower buds developed but not yet opened
- SF - leafless

It was hoped that these scale values, based entirely on visual interpretation, would help in clarification of the structure and phytosociology of the stands.

2. Soils

A soil pit was dug at a representative site near the centre of the stand, to a depth of at least 90 cm where possible. A soil sample was taken from each horizon in the profile and the thickness of each horizon was recorded, together with notes on colour, structure and moisture. Also, small soil samples were collected from the pit at depths of 8 cm, 23 cm and 90 cm and placed in air-tight tins for future weighing and drying to determine the moisture content on an oven-dry basis. Four other soil samples were taken at 23 cm depth within the stand area, to assess moisture variability. All samples were sieved through successive sieve meshes of 3/4 inch, 1/4 inch and 2 mm, and the percentage sample weight in each size-class calculated. A number of analyses were carried out on the <2 mm fraction as follows:

1. A portion of the sample was oven-dried at 105 C to constant weight. Each succeeding analysis of the sample could then be expressed on an oven-dry basis.

2. For soil texture, the percentage weight of soil in each of the following particle size classes was determined by mechanical analysis by the hydrometer method of Bouyoucos (1951) with some of the modifications proposed by Youngberg (1957):

- (a) 10 ml of 5% sodium hexametaphosphate solution was used as a dispersal agent instead of 5 ml of a 1 N solution.
- (b) The soil suspension was slaked with the dispersal agent for a minimum of 12 hours instead of 2 hours.
- (c) The suspension was agitated in a reciprocal shaker for one hour at the commencement of slaking and for a further half-hour just before transfer to the soil cylinder.

U.S.D.A. soil texture classification:

sand 2.00 - 0.05 mm diameter
 silt 0.05 - 0.002 mm diameter
 clay <0.002 mm diameter

3. Percentage moisture at Field Capacity and Permanent Wilting Point was determined with a Soilmoisture Equipment Co. 15 Bar Ceramic Plate Extractor and 5 Bar Pressure Plate Extractor, at pressures of 15 atm and 1/3 atm respectively. The difference between these two soil moisture values was taken to be the potentially Available Water.

4. A chemical analysis of the soil samples, including the following determinations, was made by the Provincial Agricultural Soil and Feed Testing Laboratory, Edmonton.

- i. available nitrogen (lb./acre)³
- ii. available phosphorus (lb./acre)³
- iii. available potassium (lb./acre)³

³ Converted to ppm

- iv. pH
- v. soil conductivity (mmhos)
- vi. a semi-quantitative estimate of free lime
- vii. a semi-quantitative estimate of sulphate
- viii. a semi-quantitative estimate of sodium

The methods were those recommended in the "Methods of Analysis of the Association of Official Agricultural Chemists"[⌘] and the U.S.D.A. Handbook No.60, "The Diagnosis and Improvement of Saline and Alkaline Soils"⁺, or modifications on these methods. Further details may be obtained from the Director of the Provincial Agricultural Soil and Feed Testing Laboratory at the University of Alberta.

For some measure of soil compaction, readings of the mineral soil surface were taken every 10 ft (3m) along the 300 ft (91m) baseline with a Soiltest Inc. Pocket Penetrometer, Model CL 700. It was found impossible to obtain meaningful penetrometer readings from some stands because of recent rainfall or a thick, spongy humus.

3. Other Observations

For a measure of grazing intensity, fecal group counts were made on a 6 ft strip along the 300 ft baseline, as far as possible recording only those feces which appeared to be not more than a year old. With a little practice, the feces of all the ungulates could be distinguished, except those of mule deer and young elk. Assistance in identifications was given by technicians of the Canadian Wildlife Service, Edmonton.

⌘ A.O.A.C., 1955

+ Soil Salinity Laboratory Staff, 1954

Finally, the exact location and elevation of each stand were recorded and notes made on qualitative and unsampled stand features.

About 30 additional grassland areas were briefly described as time permitted, the notes consisting of species lists and rough Cover-abundance estimates of each species. A soil core was also taken in each area in order to obtain an indication of the soil type. Most of these additional areas were either too small to merit full study or were of minor interest owing to the lack of uniformity or to disturbances, *etc.*

Environmental Stations

One environmental station was set up in an apparently representative grassland site in each Park (Figs. 2, 4, and 5, p. 9, 11 and 12), and their readings used as standards to assist in the evaluation of microenvironmental data. The environmental readings taken at the Jasper and Waterton Lakes stations included: (a) soil temperature and moisture readings at depth of 8, 23 and 60 cm with thermistor probes and a Soiltest Inc. Soil Moisture Ohmmeter, Model MC-300A; (b) continuous air-temperature recordings at 4 ft with a drum-recording thermograph in a Stevenson's shelter; (c) maximum and minimum air-temperatures as a check on the thermograph readings; (d) recordings of rainfall with a standard (Dept. of Transport) Meteorological Branch Rain Gauge.

The readings at the Banff station were taken similarly, except that no soil moisture or temperature readings could be taken because of the lack of a third Soiltest meter.

The environmental stations were set up in late June or early July, 1967, and their instruments read weekly until the end of August, 1968.

Standing Crop Studies

In order to assess relative primary productivity, seven sites representative of the major grassland types in this study were selected for standing crop estimates (Figs. 2-5, p. 9-12). During May, 1968, before the commencement of discernible growth, 10 wire cones were placed randomly at each of these sites to protect the enclosed area from grazing by ungulates. Each cone was made from a semi-circle of 2-inch wire mesh and enclosed a ground area of slightly more than 10 ft². Five of these cones were removed in late July and the protected areas clipped within a metal ring enclosing an area of exactly 9.6 ft². All living, non-woody vegetation together with new growth of woody vegetation was clipped as close to ground level as possible and the clippings sorted into 2 categories: (a) grasses and sedges (b) other herbs and shrubs. The other five cones were removed in late August, 1968, and the same clipping procedure followed. The clippings were air-dried to constant weight at room temperature (about 25 C) and the weighings recorded in lb./acre (1g/9.6 ft² = 10 lb./acre = 11.2 kg/ha). It was considered that the July

clippings represented the peak above-ground standing crop for most species.

Sampling of Intensive Study Sites

Following the preliminary classification of 1967 stands into grassland types by means of ordination techniques, three sites were selected for more intensive studies during the summer of 1968 (Figs. 2, 4 and 5, p. 9, 11, 12). These areas were chosen to investigate the effects of small-scale environmental factors on the vegetation within a narrowly-prescribed area while keeping larger-scale environmental factors constant.

The three sites were sampled as follows:

1. Badlands, Waterton Lakes National Park (Fig. 25, p. 156): an area of relatively undisturbed fescue prairie on glacial till benches overlooking the Waterton River valley. The gently-rolling topography, probable uniformity of the C horizon and lack of any abrupt vegetational or topographical discontinuities made this an ideal location for the purposes described above.

Seven stands, each 100 ft x 100 ft, were sampled in early August, 1968, their centres lying along a 1,500 ft (457m) transect running roughly N-S across the Badlands. Another stand had previously been sampled in the same area at the end of June. A Dumpy level and a Philadelphia rod were used to measure local elevation-al changes at 1 ft (.3 m) intervals along the transect

for the whole 1,500 ft.

These stands were sampled sequentially with 1 m x 1 m random quadrats until a previously-fixed, minimum standard error for the cover of the most important grass species was obtained. The standard error was set at 15% of the mean cover value. After several stands had been completed, it was found that extending this sampling to 20 quadrats achieved the desired precision for the Dominant species and at the same time gave an adequate sample of the less abundant species.

Fifty cover points were recorded within each quadrat, with a fixed pattern of five sets of pins in a ten-pin point quadrat frame. A pin was lowered at each cover point and the species touched by the point of the pin recorded. The cover of each species in the stand was calculated as a percentage of the total possible "hits". Every species present in a quadrat was assigned a Cover-abundance value (p. 33), and these values used to build up a comprehensive species list for the stand. Thus, comparison of vegetation could be made with the stands sampled in 1967.

Soil temperature at a depth of 20 cm was measured with a 20 cm dial probe thermometer at the centre of each of the first 10 quadrats between 11 AM and 1 PM on the day of sampling and the air temperature at 4 ft recorded at the same time with a shielded alcohol-in-glass thermometer.

Soil samples at a depth of 20 cm were taken from the centres of five of the first 10 quadrats. These samples were taken as follows; one as close as possible to the stand centre and the other four as close as possible to the centres of the four quadrants. They were kept in sealed tins and later analysed for oven-dry moisture content.

Soil temperature and moisture data were later corrected for date of sampling by using the data obtained from the nearby environmental stations.

Measurements of slope angle and slope aspect were made where necessary in the stand to form, along with the transect profile, an accurate picture of the stand's topography.

As a measure of grazing, fecal group counts were made on a 6 ft (2 m) wide strip along the 100 ft baseline and a 100 ft line bisecting the stand at right angles to the baseline.

Finally, a soil pit was dug at the centre of the stand to a depth of at least 90 cm. Soil samples were taken from each horizon and the thickness, colour and appearance of each horizon recorded. These samples were later air-dried, sifted into two fractions, *i.e.*, > and < 2 mm diameter, and analyses carried out on the < 2 mm fraction as on the samples collected in 1967 (p. 36-38). In addition, determinations of total carbon were carried out by the Alberta Soil Survey Laboratory, using an induction furnace for total combustion and measuring evolved

carbon dioxide volumetrically. The same laboratory determined inorganic carbon by measuring volumetrically the carbon dioxide evolved on addition of hydrochloric acid and calculating the result as calcium carbonate. The difference between total and inorganic carbon gave a measure of the organic carbon content.

2. "Hay Meadow" area, Waterton Lakes National Park (Fig. 28, p. 184): an area of low-lying meadows near "Knights" Lake and the Dardanelles, showing the vegetational zonation from fescue prairie on the drier areas to sedge meadows in the more mesic areas.

Between June 21 and June 27, 1968, six stands were sampled in the same way as the Badlands stands, except that no transect line was used, and the topography was so flat that no slope angle or aspect measurements were possible.

These six stands formed a vegetational series from fescue prairie to almost pure sedge meadow, a zonation which would, presumably, be correlated with certain edaphic factors and with soil moisture content.

3. "Henry House flats", Jasper National Park (Fig. 31, p. 215): an area of arid, very heavily grazed grassland and lodgepole pine savanna on sandy soils in the Athabasca River valley about 8 miles N of Jasper townsite.

Six stands were sampled between June 14 and June 19, 1968, in the same way as stands of the "Hay Meadow" site. The stands were chosen so as to investigate the correlations between vegetation and certain microenvironmental factors

associated with the transition from pine forest to grassland.

It was hoped that data from these three intensively studied sites would elucidate relationships between local species distribution and abundance and certain microenvironmental factors within the two most distinctive grassland types in this study, *i.e.*, the fescue prairie in the eastern part of Waterton Lakes National Park and the xeric grasslands in the main valleys of Jasper National Park.

CLIMATE, SOIL TEMPERATURE AND MOISTURE AT THREE GRASSLAND SITES

Although data from four meteorological stations in the study areas have already been discussed (p. 15), these stations are not in natural grassland. Anthracite was closed in spring, 1962, and at about the same time Waterton Park Headquarters ceased to record any data except precipitation. During the study period, the main meteorological station in Waterton Lakes National Park was therefore at Waterton Lakes Ranger Cabin.

Data on air temperature and precipitation were available for the study period from Banff, Jasper and Waterton Lakes Ranger Cabin meteorological stations and from temporary Banff and Jasper environmental stations which were set up in selected grassland areas (see Methods, p. 39). The Jasper environmental station was in "*Koeleria-Calamagrostis montanensis* Grassland" close to stand 42,

and the Banff environmental station was close to stand 27 in grassland related to *Koeleria-Calamagrostis montanensis* Grassland. As the Waterton Lakes Ranger Cabin Meteorological Station was in a suitable grassland area (*Festuca-Danthonia* Prairie), the data from this station (max/min temperatures and rain gauge readings) were supplemented by adding a Coleman moisture meter and a drum-recording thermograph.

Weekly air temperature fluctuations were greatest during the winter at all stations (Fig. 7). The same weather trends were shown at all stations, evidently because of the same air mass and consequent weather changes. The summer of 1967 was much warmer than that of 1968. Mean weekly temperatures for 1967 and 1968 during the period July - August at Waterton Lakes Ranger Cabin were in the ranges 60-65 F and 55-60 F respectively. At Jasper Meteorological Station, the mean August temperatures were in the range 55-65 F in 1967 and 45-55 F in 1968 (Fig. 7).

Precipitation was much lower in the summer of 1967 than in 1968, especially in Banff and Waterton. Total June - August precipitation in 1967 and 1968 was (inches) 3.44 in 1967 and 5.61 in 1968 at Banff, 5.51 and 5.88 at Jasper and 7.54 and 13.08 at Waterton. Temperature and precipitation data from Banff, Jasper and Waterton meteorological stations and Jasper environmental

Figure 7. Weekly fluctuations in maximum, mean and minimum air temperatures at five weather stations; July, 1967 to August, 1968.

- (a) Banff meteorological and environmental stations.
- (b) Jasper meteorological and environmental stations.
- (c) Waterton Lakes Ranger Cabin meteorological station.

FIGURE 7 A BANFF

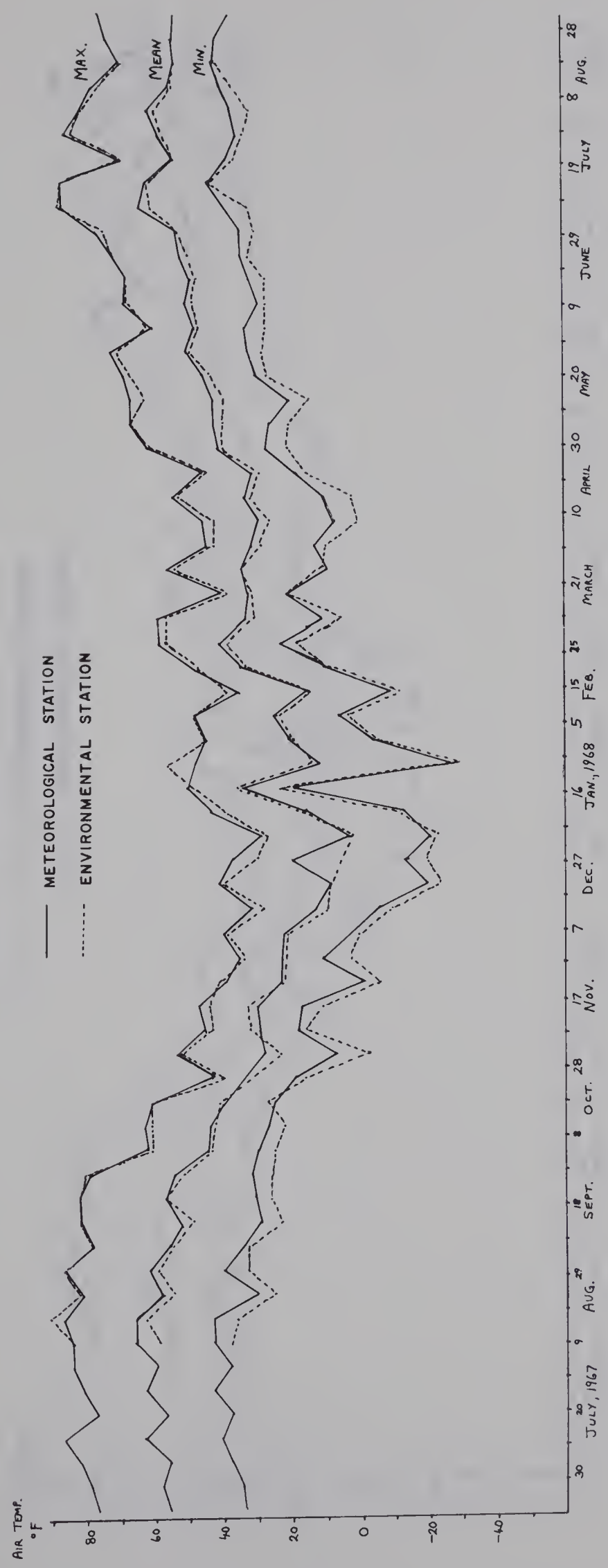


FIGURE 7 B JASPER

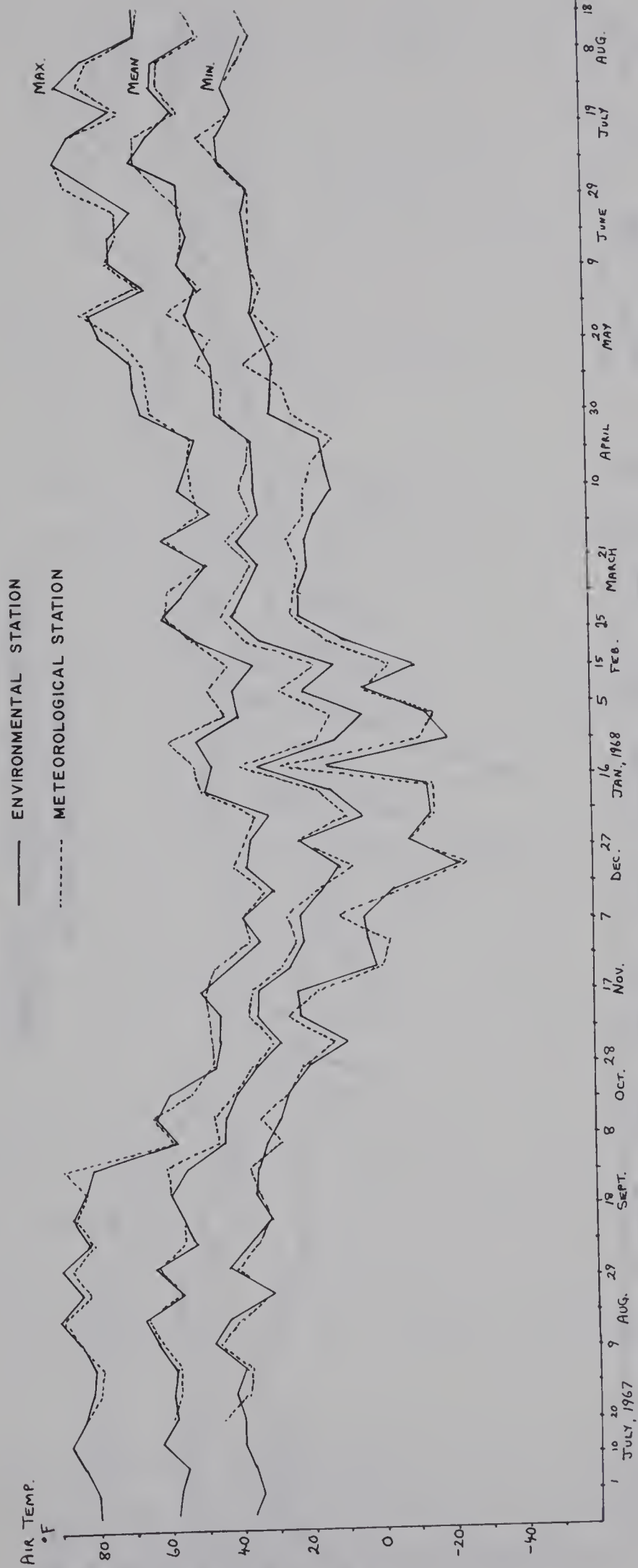
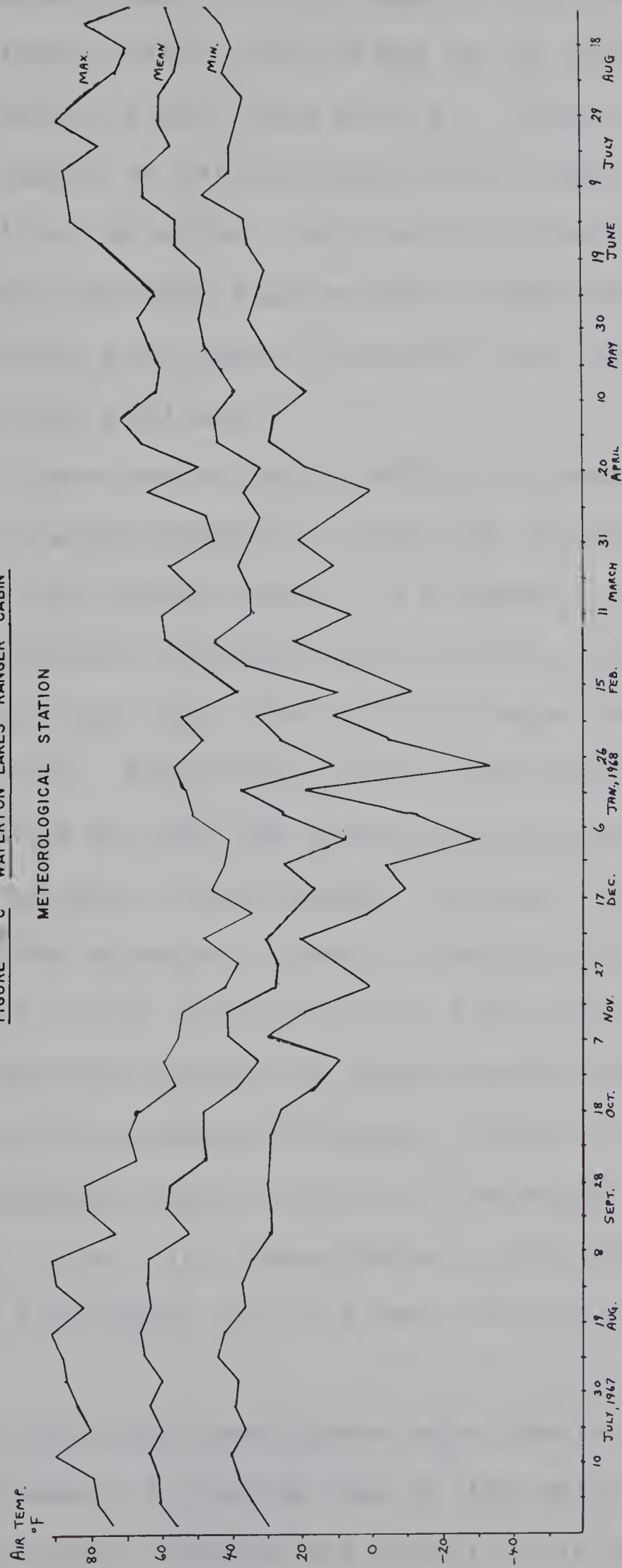


FIGURE 7 C WATERTON LAKES RANGER CABIN

METEOROLOGICAL STATION

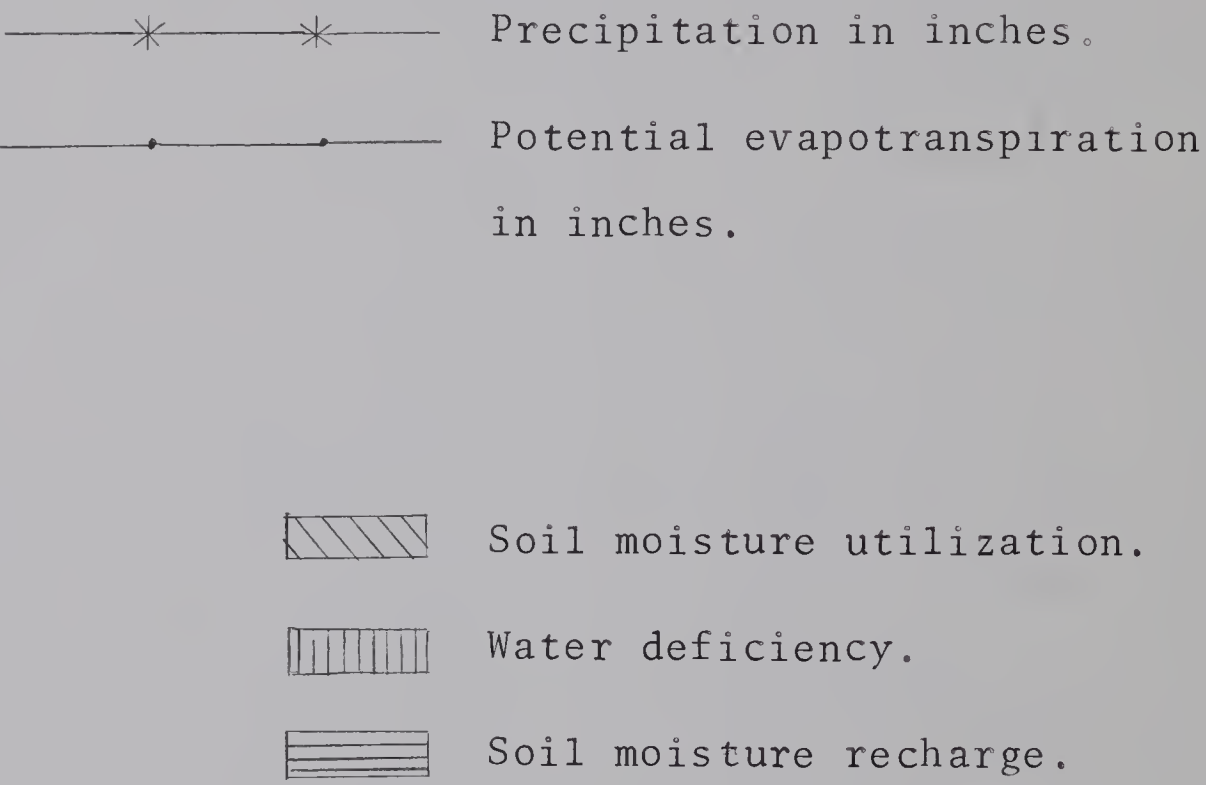


station for the period June, 1967 to August, 1968, are shown in water balance charts constructed by the method of Thornthwaite and Mather (1957) (see Fig. 8). These data confirm that the summer of 1967 was much drier than that of 1968, especially at Waterton. As the precipitation data from Banff environmental station were incomplete, no measurements having been made of snowfall, no charts were prepared for this station.

At Waterton, there was no water deficit in summer 1968 but there were approximately 2 months of drought in summer 1967, the water deficit being 7.17 inches. Although there were water deficits in late summer in both years at the Banff and Jasper stations, the deficits began several weeks earlier in 1967. Water deficits in late summer of 1967 were replenished by fall and winter precipitation by late December at Waterton, late January at Jasper, and early March at Banff. From November to March, precipitation, mostly as snow, was 12.52, 4.31, 4.15 and 5.65 inches respectively at Waterton, Banff and Jasper meteorological stations and Jasper environmental station. There was more snow at the environmental station than at the meteorological station in Jasper. Also, air temperatures, especially the maxima were about 2 F higher at the former station in the winter months.

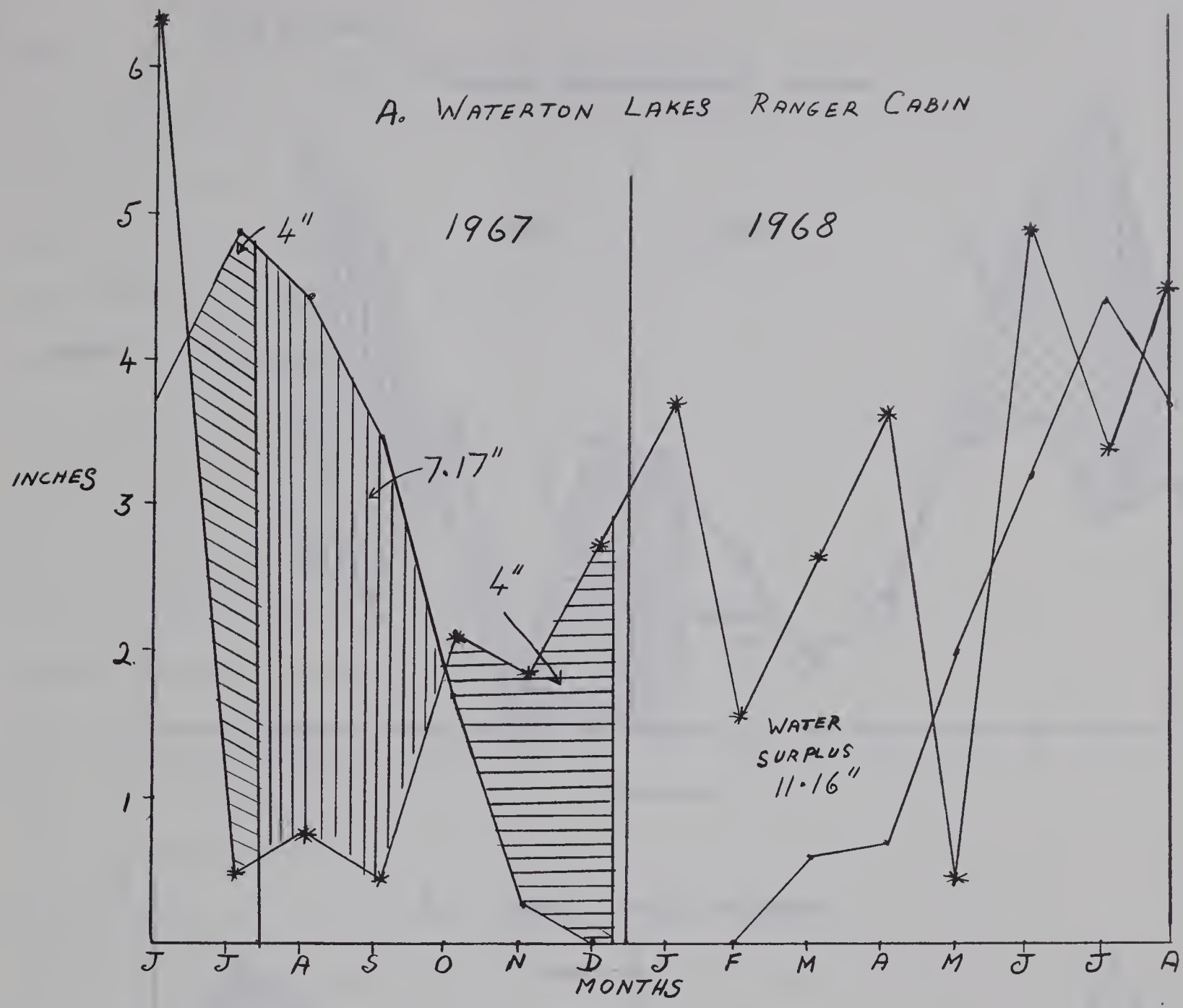
At Banff, the minimum temperatures were generally lower at the environmental station than at the meteorological station, probably because the latter is in a

Figure 8. Climatic diagrams for four weather stations; June, 1967 to August, 1968.



- A. Waterton Lakes Ranger Cabin.
- B. Jasper Met. Station.
- C. Jasper Environmental Station.
- C. Banff Met. Station.

A. WATERTON LAKES RANGER CABIN



B. JASPER MET. STATION

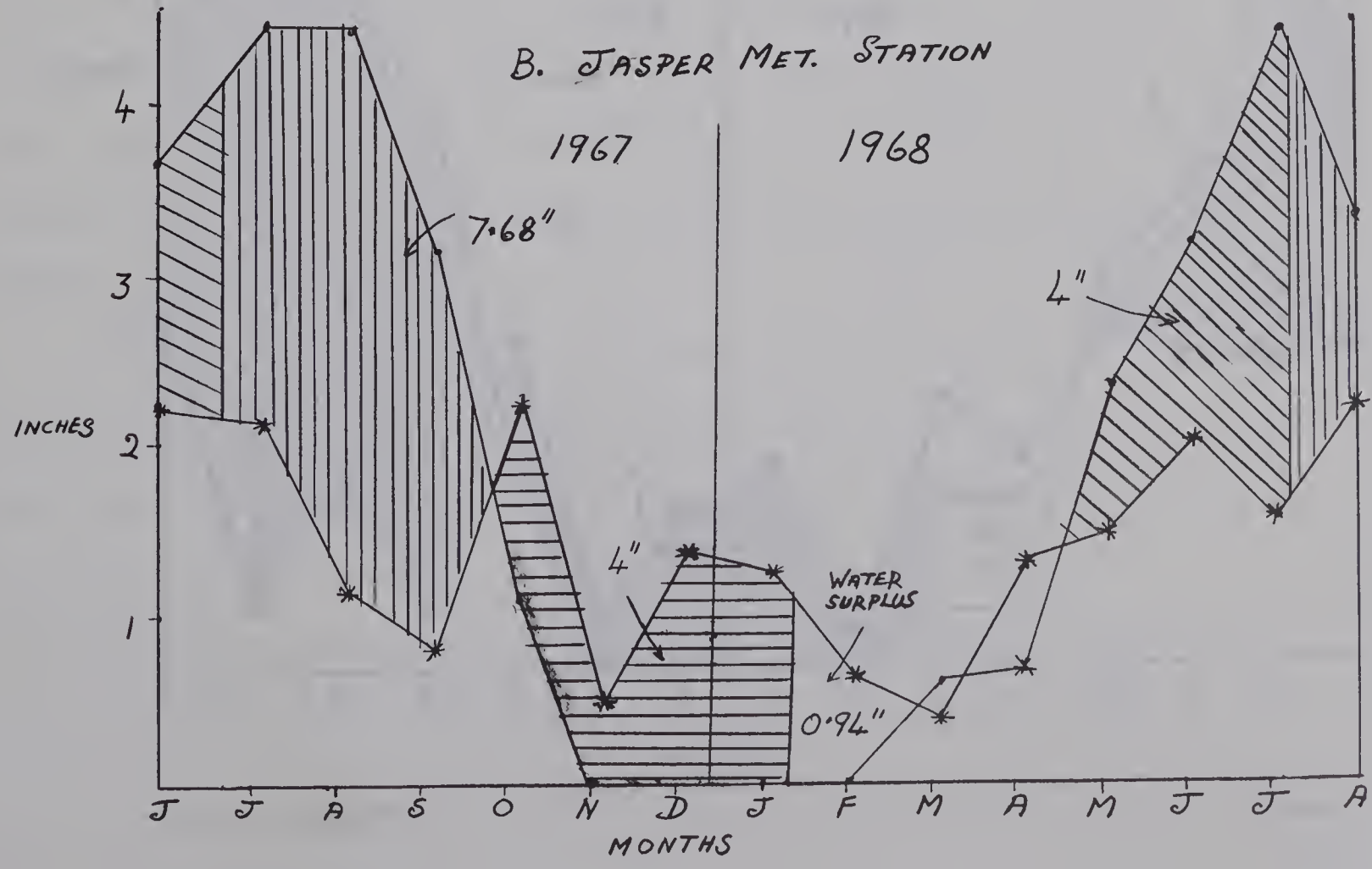
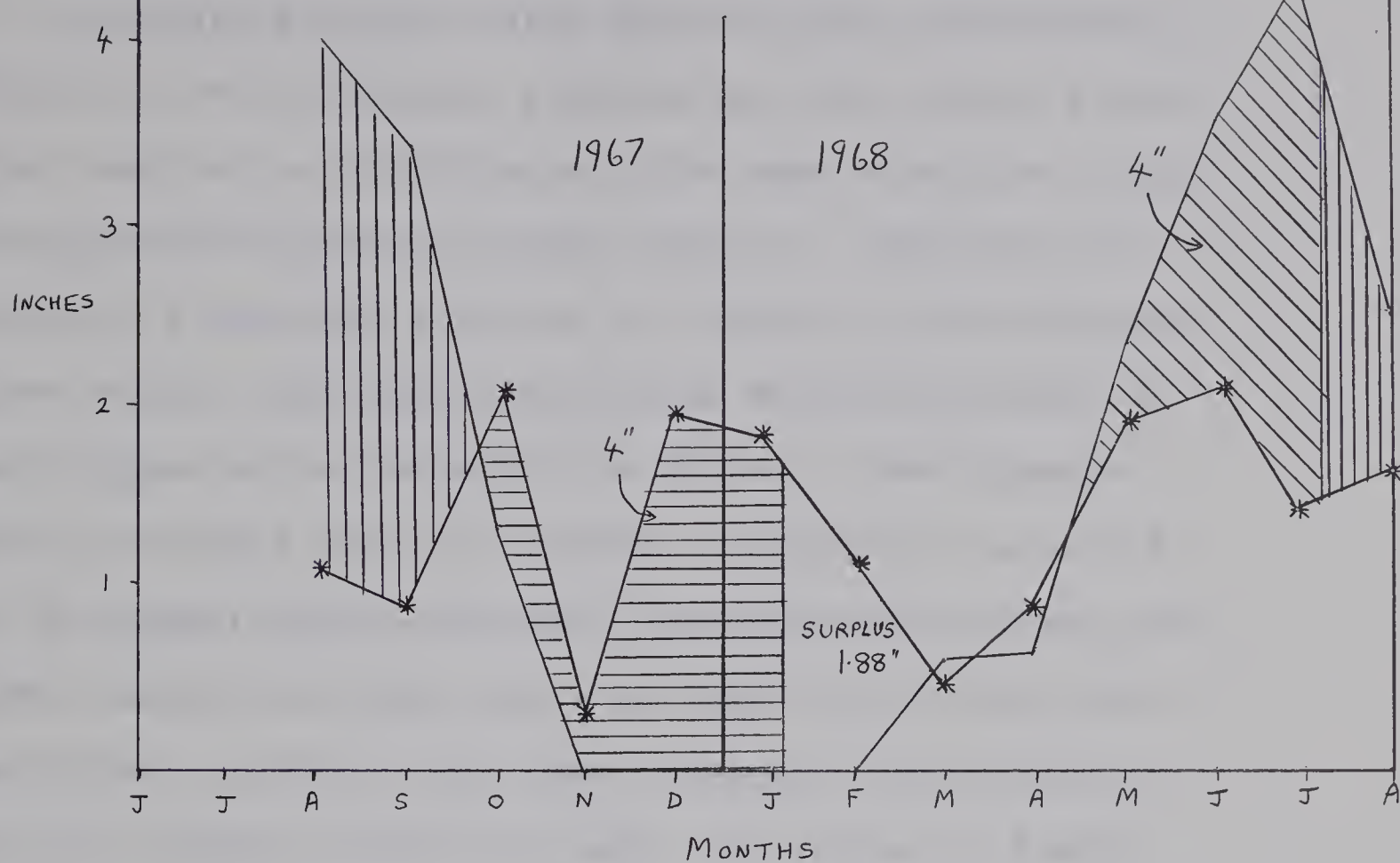
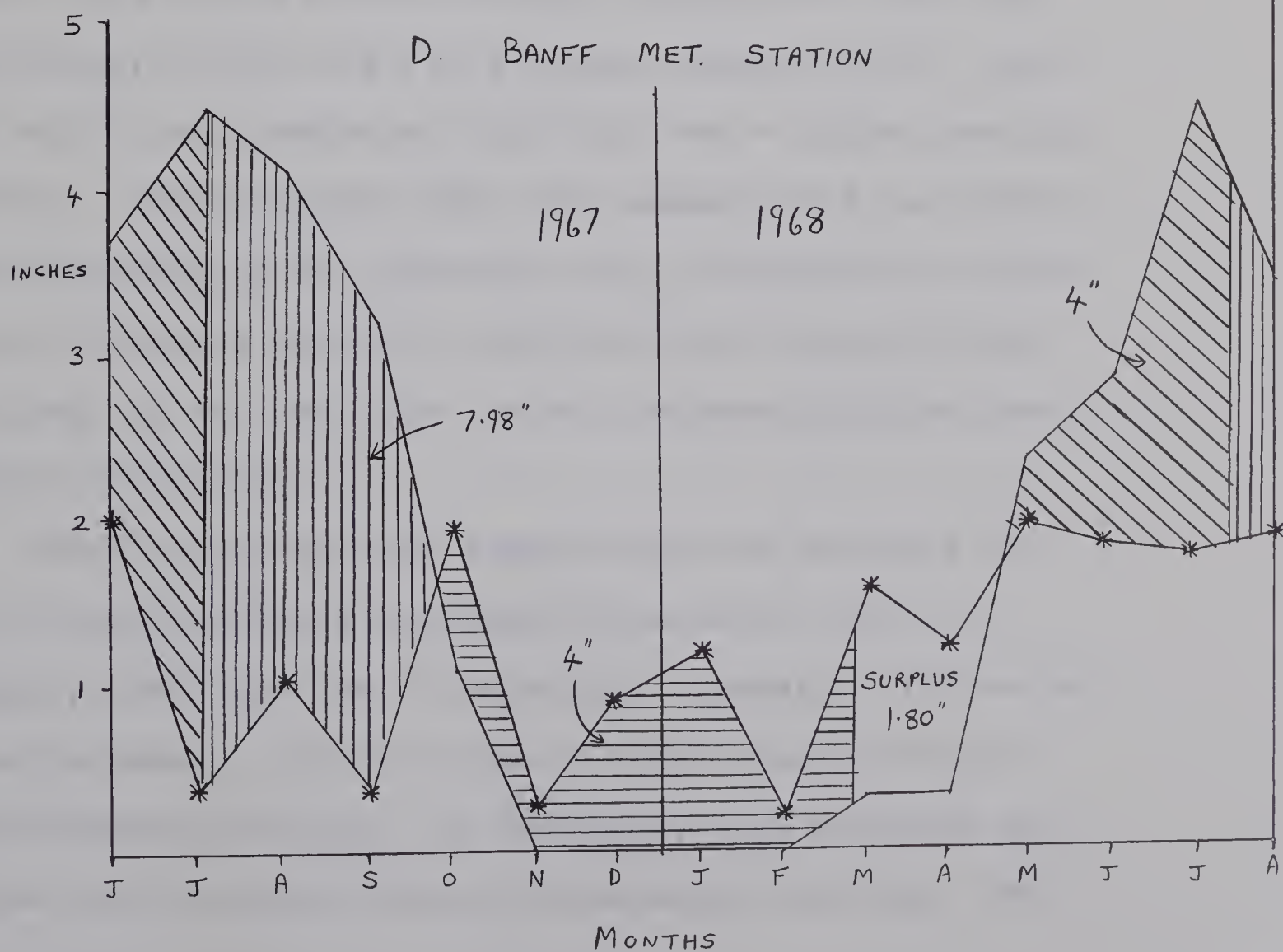


FIG. 8 (CONT.)

C. JASPER ENVIRONMENTAL STATION



D. BANFF MET. STATION



more protected position at Banff townsite.

Although Waterton Lakes Ranger Cabin and Waterton Park H.Q. meteorological stations are only about 4 miles apart and are at approximately the same elevation, their precipitation patterns differ greatly. The Park H.Q. station in Waterton townsite is further up the Waterton River valley than the Ranger Cabin station, and had a much higher winter snowfall in 1967-8. From November to March, snowfall was 17.91 inches at Park H.Q. and 12.52 at the Ranger Cabin. However, precipitation during the summer months was much lower at Park H.Q. in both 1967 and 1968. In 1967, from June to August, precipitation was 5.6 inches at Park H.Q. and 7.54 inches at Ranger Cabin, and in 1968 precipitation figures for the same period were 10.63 and 13.08 inches respectively. Over the whole year, Waterton Park H.Q. has a higher precipitation. These figures show that amounts and patterns of precipitation in the mountains vary considerably within short distances and it is doubtful how "typical" the readings at any one site are of the precipitation even within one valley.

Weekly data on soil temperature and moisture at 8, 23 and 69 cm were available from July, 1967 to August, 1968 from the Waterton environmental station and from September, 1967 to August, 1968 from the Jasper Environmental station. At Waterton, soil moisture was below the Permanent Wilting Percentage from July, 1967

to late January, 1968 at all three depths (Fig. 9). During a warm period in January, 1968, melting snow restored soil moisture almost to Field Capacity. In the middle of July, 1968, soil moisture at all three depths dropped sharply to below Permanent Wilting Percentage and remained below this point until heavy precipitation in early August restored soil moisture to close to Field Capacity. This drought period is not apparent on the water balance diagram. Light rains during the 1967 and late July - early August 1968 drought periods seem to have had little effect on soil moisture. At 69 cm, soil moisture was much higher than at 8 or 23 cm and remained close to Field Capacity until late July, 1968.

In summer, soil temperature fluctuated most at 8 cm and least at 69 cm but in winter was approximately 32 F at all three depths, except during the brief period of thaw in late January, 1968 when the temperature at 8 cm rose to 36 F.

At Jasper environmental station, the soil moisture was well below Permanent Wilting Point at all depths, from August, 1967 to August, 1968 except for short periods in October, 1967 and March - April, 1968, when the reading at 8 cm was above this point, perhaps because of heavy rains and spring thaw respectively. Soil moisture at 23 cm was usually lower than at 8 or 69 cm. This indicates a discontinuity in soil moisture and perhaps more lateral than vertical movement of water at 69 cm. Thus,

Figure 9. Weekly fluctuations in soil moisture, soil temperature and precipitation at Waterton and Jasper environmental stations; July, 1967 to August, 1968.

(a) Jasper

(b) Waterton

FC = Field Capacity %

PWP = Permanent Wilting %

Precipitation:  = rain,  = snow

as inches of precipitation.

Downward arrows (soil moisture) indicate that the true values were probably lower than those recorded.

FIGURE 9 A JASPER

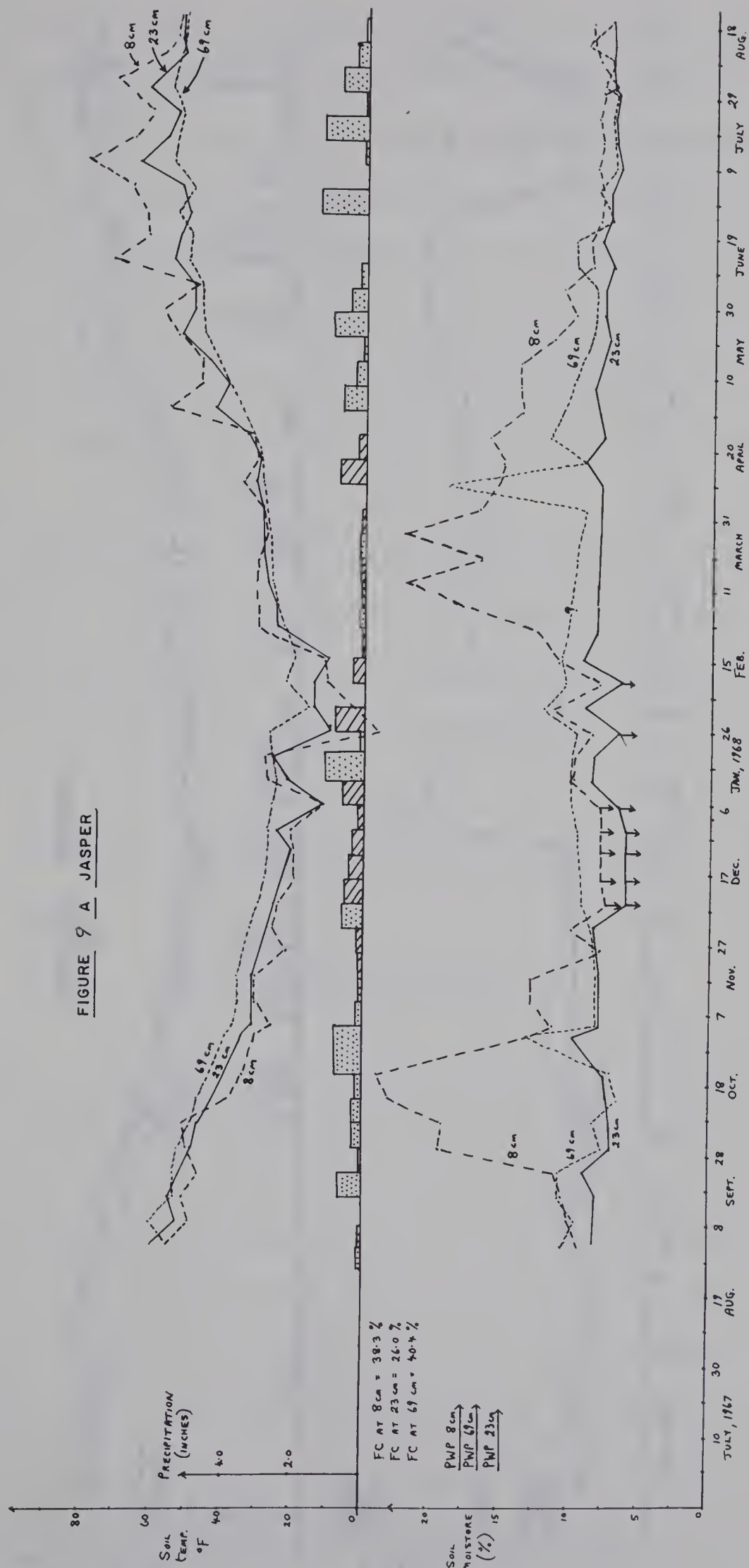
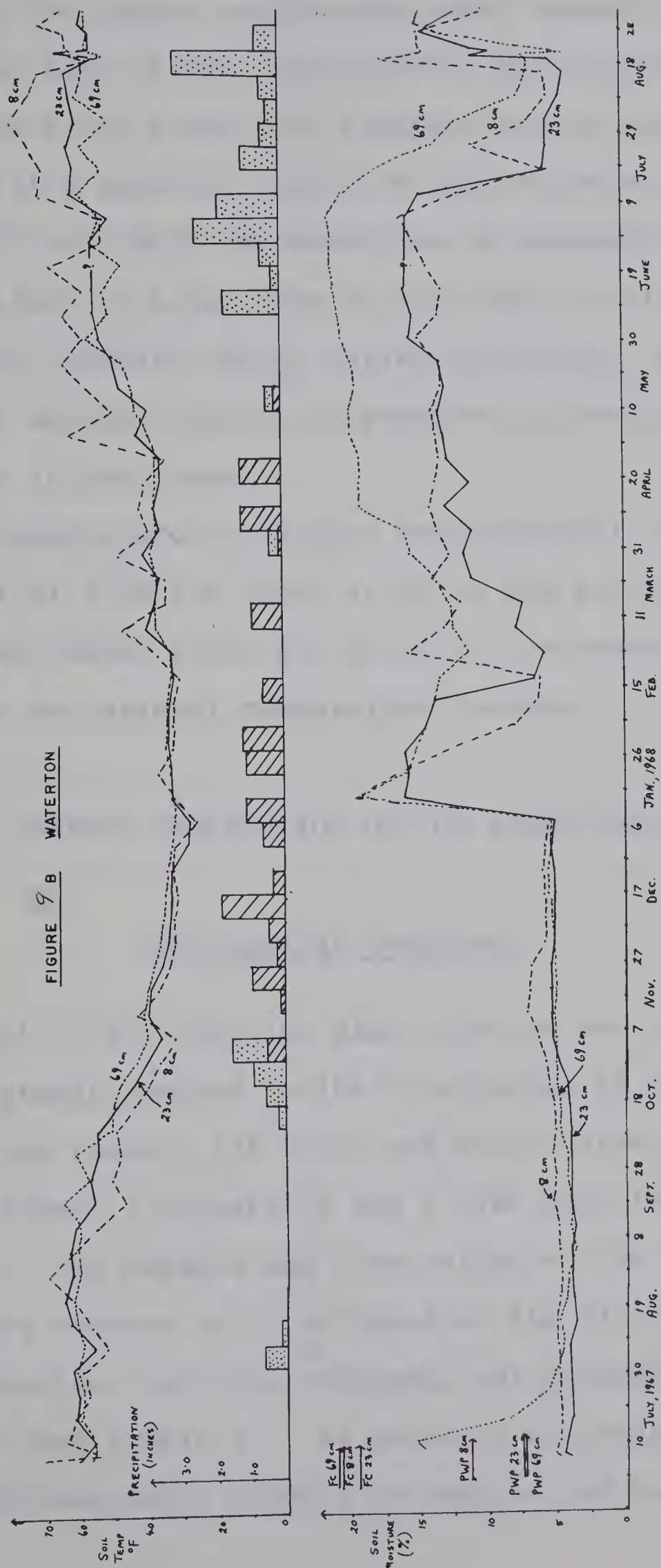


FIGURE 9 B WATERTON



the soil at the Jasper station was under drought conditions during most of the study period, and considerable rainfall which was especially frequent during summer, 1968 had little apparent effect on soil moisture content at 23 and 69 cm. With the exception of unusually wet years, moisture is always low in the sandy, well-drained soils of the Athabasca River valley grasslands, and large water deficits are to be expected in middle and late summer in most years.

Soil temperatures at Jasper environmental station varied most at 8 cm and least at 69 cm and at both Waterton and Jasper there was at 69 cm a pronounced lag in response to seasonal temperature changes.

GENERAL DESCRIPTION OF THE VEGETATION

The Vascular Component

A total of 281 vascular plant species was recorded in the 51 stands sampled in 1967, including 49 grasses, 25 sedges and rushes, 184 forbs and dwarf shrubs, 18 shrubs, 2 ferns, 2 horsetails and 1 club moss (Appendix 4, p. 317). Two hundred and forty-eight of the 281 species were present in 20 or fewer of the 51 stands and only one species, *Koeleria cristata*, was present in more than 40 of them (Table 3). As *Koeleria* was absent from nine of the most mesic stands, no species can be considered

TABLE 3. TOTAL NUMBERS OF SPECIES IN 20% PRESENCE CLASSES.

Class Presence %	1 0-20	2 20-40	3 40-60	4 60-80	5 80-100	Total
Grasses	30	11	5	2	1	49
Sedges and rushes	21	4	0	0	0	25
Forbs and dwarf shrubs	135	26	15	8	0	184
Ferns, club mosses and horsetails	4	0	1	0	0	5
Shrubs	14	3	0	1	0	18
Total	204	44	21	11	1	281

as Constants for these grasslands. Only the following species had mean cover values of over 3% (the mid-point of the "1" value range on the Cover-abundance scale; see Methods, p. 34): *Festuca scabrella* (6.0), *Poa pratensis* (5.8), *Koeleria cristata* (5.0), *Festuca idahoensis* (4.6), *Danthonia parryi* (3.1), *Stipa richardsonii* (3.1), *Antennaria nitida/rosea*⁴ (6.9). These figures illustrate the extreme vegetational diversity of the low-elevation grasslands. Two pairs of stands, Nos. 34 and 37, and Nos. 22 and 48, had not a single vascular species in common.

The diversity of the grasslands was apparent not only in their composition but also in their structure. In Waterton most of the grasslands were in the "short grass formation class" (Fosberg, 1967). The total cover of all vascular plant species (calculated from Cover-abundance values) in the Waterton grasslands was approximately 105%, with shrubs making up only 2% of this value total. These grasslands generally had the three following strata: a tall forb-bunch grass stratum (up to 70 cm high), a small forb-grass understory (up to 25 cm high), and a mat-like ground cover (up to 3 cm high).

Most of the grasslands at low elevations in Banff and Jasper were of the "steppe formation class" (Fosberg, 1967)

and at

⁴Indistinguishable except when flowering and usually found only in vegetative state.

high elevations were of the "shrub savanna" or "short grass" formations. The mean total cover of vascular plant species was approximately 100% in Banff and 80% in Jasper, with shrubs making up 8% and 3% of the respective totals. Strata were ill-defined and usually only two in number, corresponding to the two lower strata in Waterton.

Many of the stands at higher elevations, especially in Banff, had a well-defined, open, shrub stratum, usually much less than 100 cm high, and a few of these stands also had a tall forb-bunch grass stratum similar to that of the Waterton grasslands. About 20 species were confined to and usually prominent in the 20 Waterton stands, thus illustrating a floristic difference between the Waterton grasslands and those in the more northern Parks. The most prominent species apparently exclusive to Waterton were *Festuca idahoensis*, *Danthonia parryi*, *Lupinus sericeus*, *Geranium viscosissimum*, *Lithospermum ruderales*, *Monarda fistulosa*, *Antennaria pulcherrima*, *A. umbrinella* and *Chrysopsis villosa*. These species are not necessarily absent from Banff and Jasper; for example, *Chrysopsis* is quite common on dry, open slopes on Tunnel Mountain, Banff. The only other prominent species confined to the stands in one of the Parks was *Senecio cymbalarioides* which occurred in 13 of the 16 Jasper stands. The following species were notably absent from the Jasper stands: *Festuca scabrella*, *Stipa columbiana*, *Hedysarum sulphurescens*, *Penstemon confertus*, *Aster laevis* var. *geyeri*, *Senecio canus*

and *Solidago missouriensis*. Two prominent Banff and Jasper grasses, *Elymus innovatus* and *Festuca saximontana*, were absent from Waterton stands. Of the shrubs, only one, *Potentilla fruticosa*, was an important constituent of much of the grassland.

The Bryophyte and Lichen Component

Bryophytes and lichens were generally uncommon, and only four species were found with any regularity (Appendix 5, p. 324). Two small turf mosses, *Tortula ruralis* and *Ceratodon purpureus*, were present in 30 and 13 of the 51 stands respectively, usually restricted to areas with low vascular plant cover, and had mean cover-values of 1.2 and 0.1%. *Abietinella abietina*, a feather moss and *Peltigera canina*, a foliose lichen, were also common, being present in 11 and 24 stands respectively, and having mean cover values of 0.2 and 0.5%. *Abietinella* was usually found in the shade of small shrubs and in damp spots, whereas *Peltigera* was more commonly associated with arid areas of low plant cover.

A prominent feature in many of the arid grassland areas in Jasper Park was the presence of small, jelly-like balls of the blue-green alga, *Nostoc* sp..

ORDINATION OF 51 STANDS (1967)

Construction of the Ordination

The extreme diversity of species composition among the 51 stands sampled in 1967 indicated that more than one discrete type of grassland occurs in the three Parks. It therefore seemed desirable to classify the stands objectively, the semi-quantitative data on vascular species composition and population size (Cover-abundance value) being suitable for this purpose (Bannister, 1966).

The ordination method of continuous classification developed by Bray and Curtis (1957; *inter alia*) was selected because of its comprehensive nature, flexibility, and ease of visual interpretation. An ordination places stands in relation to one or more axes so that the distances between stands are inversely proportional to their similarity. The ordination technique then clarifies the relationships between individual stands and stand groups, and may also be used as a model upon which any variable may be plotted. Comparison of the distribution patterns of plotted variables on the ordination permits the detection of interspecific associations and other ecological relationships.

A three-dimensional ordination was constructed, based on an Index of Similarity (Bray and Curtis, 1957)

calculated from the formula:

$$\text{Index of Similarity (IS)} = \frac{200W}{A + B} \quad (\text{as a percentage})$$

where A = sum of Cover-abundance values of all species in one stand

B = sum of Cover-abundance values of all species in another stand

W = sum of Cover-abundance values the two stands have in common

This formula requires that the Cover-abundance values be treated quantitatively.

e.g. A Cover-abundance value of 4 becomes 4.0.

A Cover-abundance value of 1 becomes 1.0.

A Cover-abundance value of + becomes 0.5.

A Cover-abundance value of P becomes 0.1.

In this way, IS values were calculated for all 1,275 possible pairs of stands (Appendix 3, p. 315).

The stand with the largest sum of IS values (the most "similar" stand) was chosen as one end of the primary or X axis (Stand No. 13). The stand with the lowest IS value to No. 13 was chosen as the other end of the axis (No. 22). The X axis was then 94.6 units long (*i.e.*, 100 = IS between Nos. 13 and 22). The other 49 stands were placed on the first axis, according to their similarity to the two end stands, by means of a formula based

on the Pythagorean theorem:

$$X_a = \frac{L_x + D_a^2 - D_b^2}{2L_x}$$

where L_x = length of X axis

D_a = "dissimilarity" to stand No. 13 (100 - IS value)

D_b - "dissimilarity" to stand No. 22

X_a = distance along X axis from No. 13

The selection of the most "similar" stand as the first end-stand of the X axis is a departure from the original method of Bray and Curtis (1957) who used the most widely-separated pairs, and from the modifications of Beals (1960) and Maycock and Curtis (1960) who used the most "dissimilar" stand. It was thought that so great a diversity in flora and vegetation existed that the end stands would have relatively few species in common with the bulk of the others if the "dissimilarity" method was used. Thus, by choosing the most "similar" stand, proportionately more of the vegetational information could be utilized, *i.e.*, the more species the end stand had in common with the other stands, the more accurately they could be placed on the axis.

The "similarity" principle was then used to construct the Y and Z axes as follows. The first end stand on the Y axis (No. 30) was selected on the basis of (a) maximum dissimilarity to Nos. 13 and 22 and having a reasonably central position on the X axis, and (b) having a relatively high sum of IS values. Number 24

had both a high dissimilarity to No. 30 and a position close to it on the X axis (*i.e.*, gave a more natural vertical axis). Therefore, Nos. 30 and 24 formed the ends of the Y axis (94.2 units long), and all the other 49 stands were placed on this axis as described above. Finally, two more stands were selected to form the ends of a Z axis, using the same procedure, *i.e.*, the first stand having a high sum of IS values, a relatively central position on both the X and Y axes, and a high dissimilarity to Nos. 13, 22, 30 and 24. Thus, the Z axis was 93.4 units long from No. 15 to No. 48, and the other 49 stands were placed on the axis as before.

The positions of the 51 stands were then plotted on the three-dimensional ordination, with the values of X, Y and Z of each stand as co-ordinates (Appendix 6, p. 326). For convenience in plotting, both the Y and Z axes were assumed to be absolutely vertical. The three-dimensional array was then represented diagrammatically on three separate planes - XY, XZ and YZ (Fig. 10).

To test the validity of the similarity ordination technique and to compare it with the more widely used dissimilarity method of Beals (1960) and Maycock and Curtis (1960), the degree of correlation between dissimilarity values (100 - IS value) and the actual inter-stand distances on the ordination field was determined. Fifty pairs of stands were chosen at random and a simple correlation coefficient ("r") calculated between inter-stand

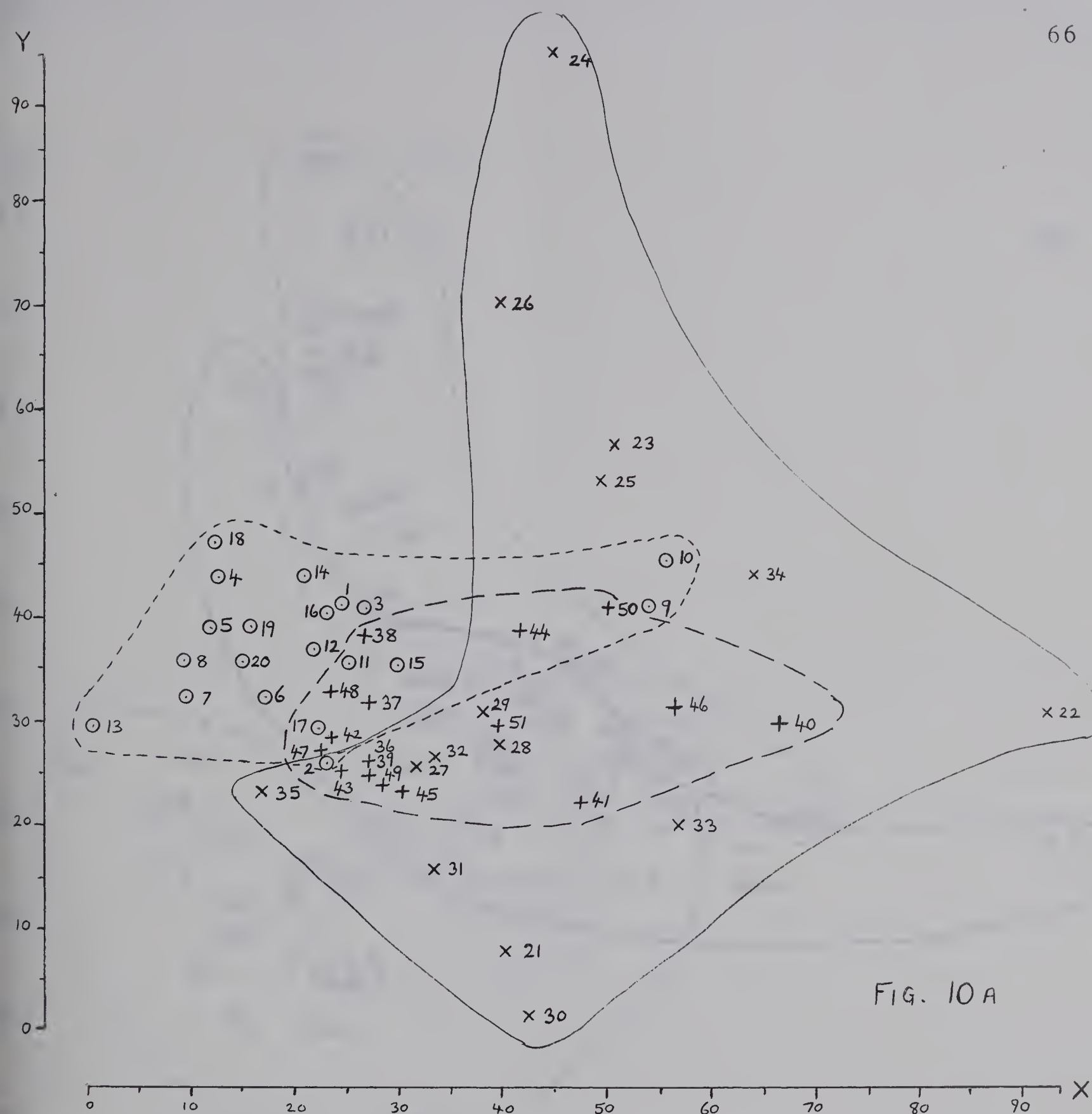


FIG. 10A

FIGURE 10A

The location of stands on the 51-stand Ordination

- A. on the XY plane.
- B. on the XZ plane.
- C. on the YZ plane.

Waterton stands (Nos. 1-20) shown as "O" and outlined as - - - - -
 Banff stands (Nos. 21-35) shown as "x" and outlined as ————
 Jasper stands (Nos. 36-51) shown as "+" and outlined as - - - - -

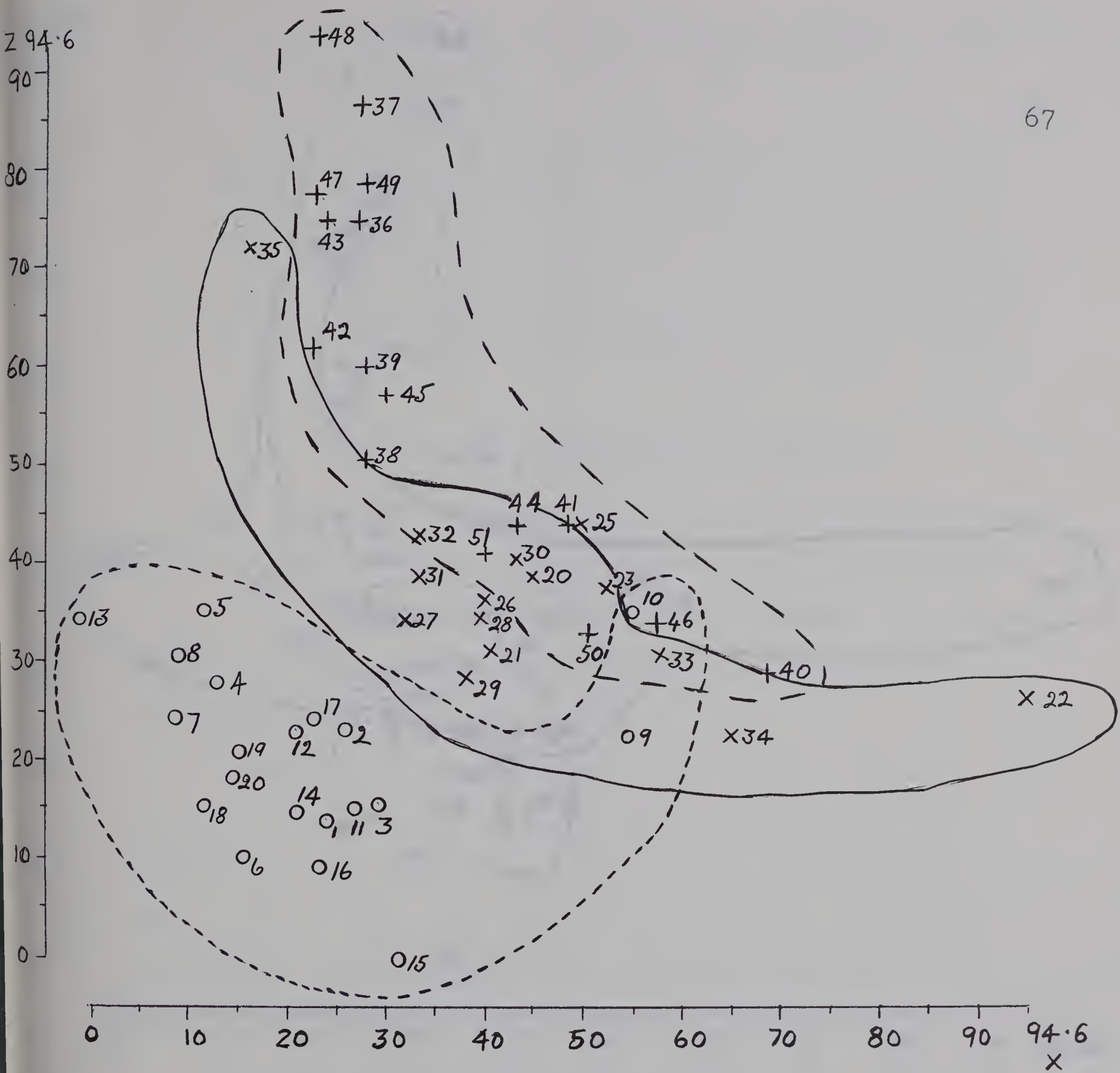


FIGURE 10 B

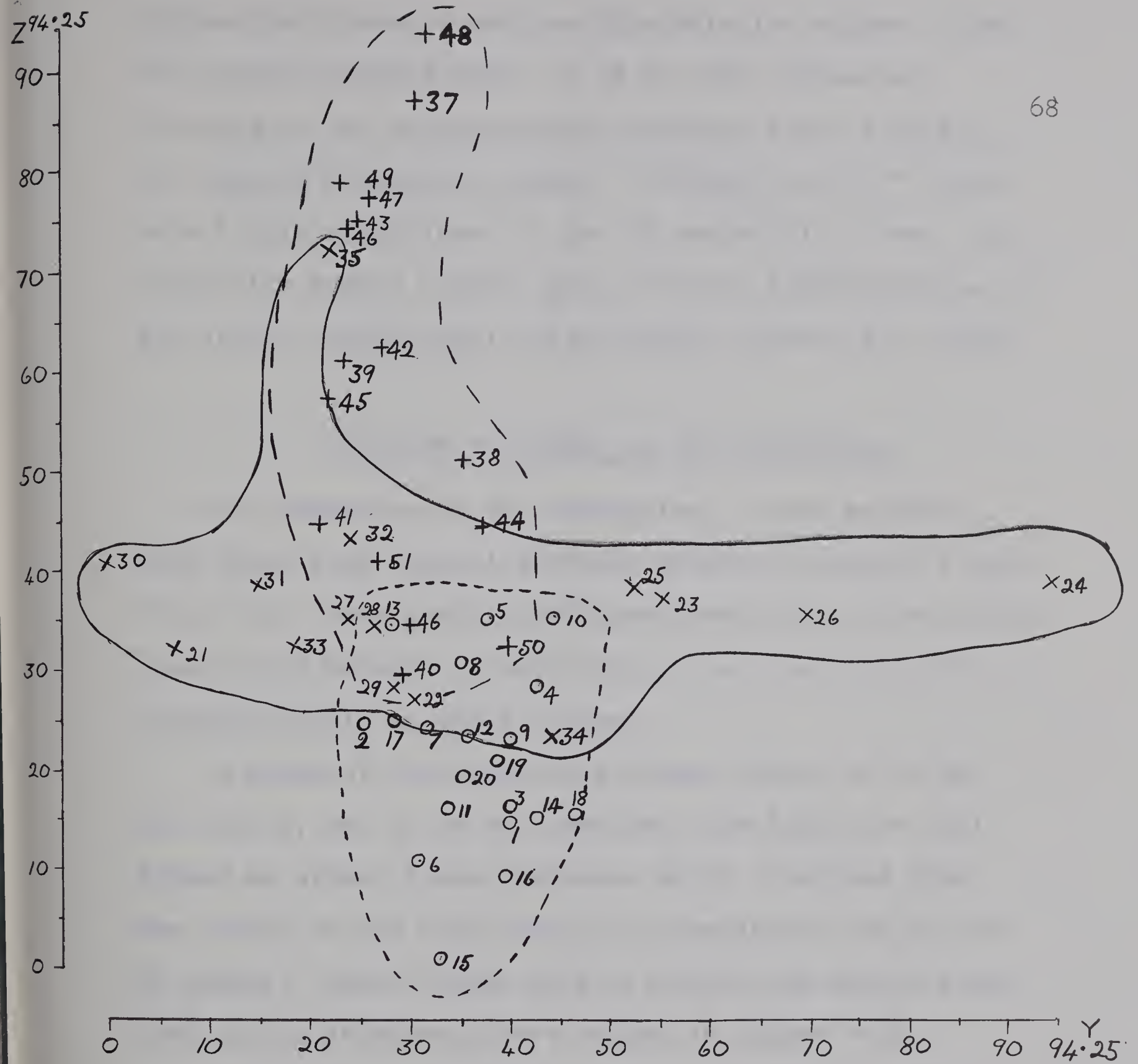


FIGURE 10C

ordination distances and the dissimilarity values. The "r" values obtained were + 0.80 for the ordination obtained by the dissimilarity technique and + 0.96 for the adopted similarity method. Although both "r" values were highly significant at the 1% probability level, the similarity method clearly gave a better representation of the actual vegetational relationships between the stands.

Position of Stands on the Ordination

On inspection of the ordination, it was evident that there were several distinct groups of related stands (Fig. 10). Most readily differentiated was a closely-knit group of 18 Waterton stands (Nos. 1 to 8 and 11 to 20), clearly visible on the XZ plane.

A group of 10 stands from Jasper, (Nos. 36 to 39, 42, 43, 45, and 47 to 49), and one from Banff (No. 35), formed an almost linear sequence which stretched from the centre to the field edge, as revealed on the XZ and YZ planes. These stands were all xeric and mostly situated in the Athabasca River valley in Jasper Park.

Two other groups formed less conspicuous, linear sequences radiating from the centre; Nos. 21, 30 and 31 from the Red Deer River valley and Nos. 23, 24, 25 and 26, four of the stands highest in elevation in Banff Park.

The remaining 15 stands, (Nos. 9 and 10 in Waterton, Nos. 22, 27 to 29, 32 to 34 in Banff, and Nos. 40, 41, 44, 46, 50 and 51 in Jasper), formed a loosely-knit group

in the centre of the field, with one of them (No. 22) fairly remote at the field edge.

Patterns of Vegetational Attributes on the Ordination

By plotting the stand Cover-abundance values for each species on the ordination field as circles of different sizes, the species that have most influence on the definition of stand groupings can be determined. Thus, species distribution patterns can be inspected, and the characteristic species composition of each grassland type described. A number of ordination diagrams showing the distribution patterns of selected species are shown on Fig. 11.

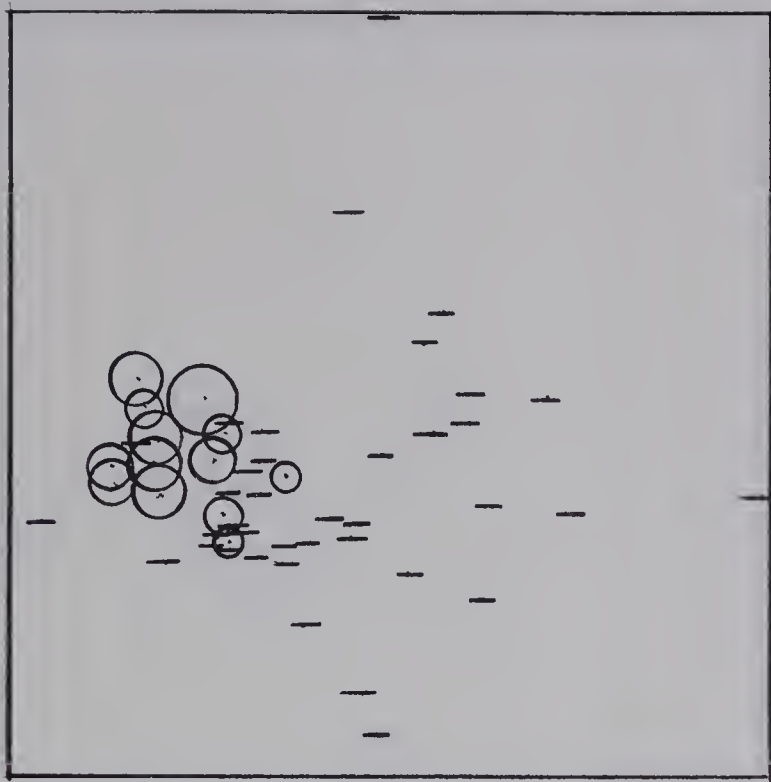
The following prominent species have the most influence on the definition of the main Waterton group of stands: the grasses *Danthonia parryi*, *Festuca scabrella*, *F. idahoensis*, *Helictotrichon hookeri* and *Stipa columbiana*; the sedge *Carex heliophila*; and the forbs *Antennaria umbrinella*, *Aster laevis* var. *geyeri*, *Chrysopsis villosa*, *Erigeron caespitosus*, *Geranium viscosissimum*, *Lithospermum ruderales*, *Lupinus sericeus*, *Monarda fistulosa* var. *menthaefolia* and *Solidago missouriensis*. Similarly, the arid grassland stands of Jasper Park are characterized by the following prominent species: the grasses *Calamagrostis montanensis* and *Koeleria cristata* and the forbs *Antennaria nitida/rosea*,⁵ *Artemisia frigida*, *Erigeron caespitosus* and *Senecio cymbalarioides*.

⁵ See footnote, p. 59.

Figure 11. The distribution patterns of 18 species on the XY and XZ planes of the 51-stand ordination.

Progressively larger circles represent Cover-abundance values of P, +, 1, 2, 3, 4 and 5; Absence from a stand represented by a dash.

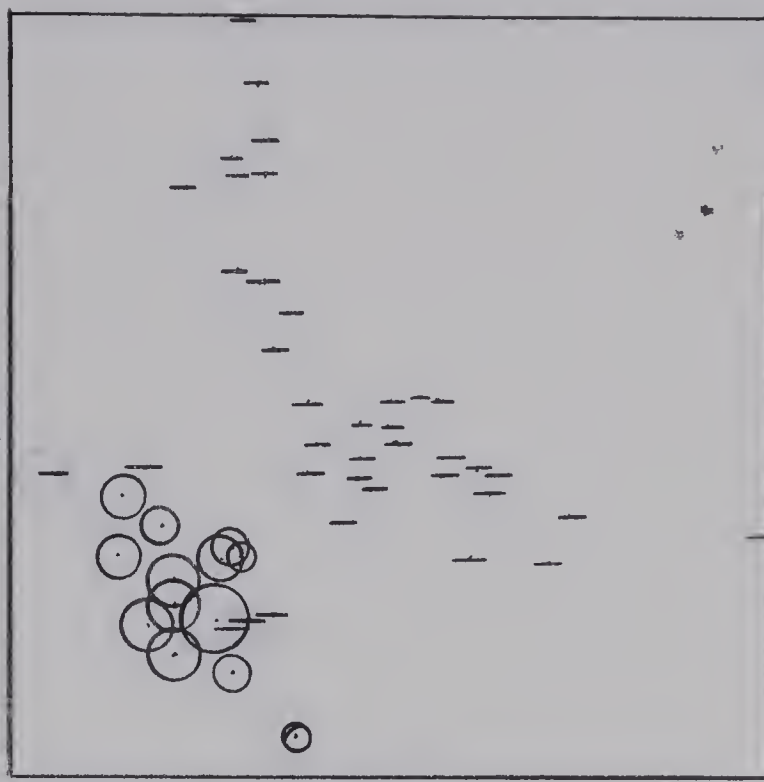
Y



X

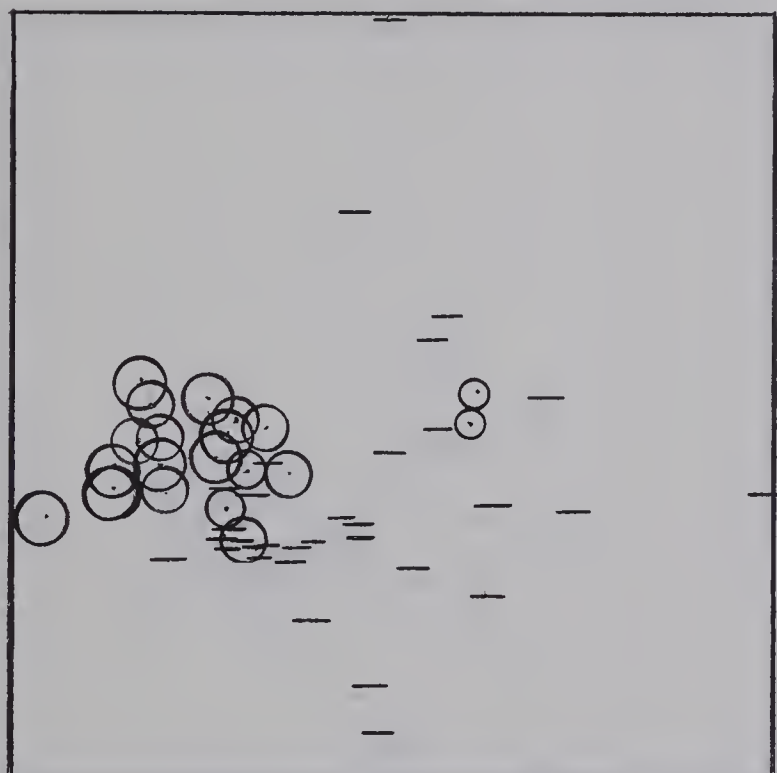
DANTHONIA PARRYI

Z



X

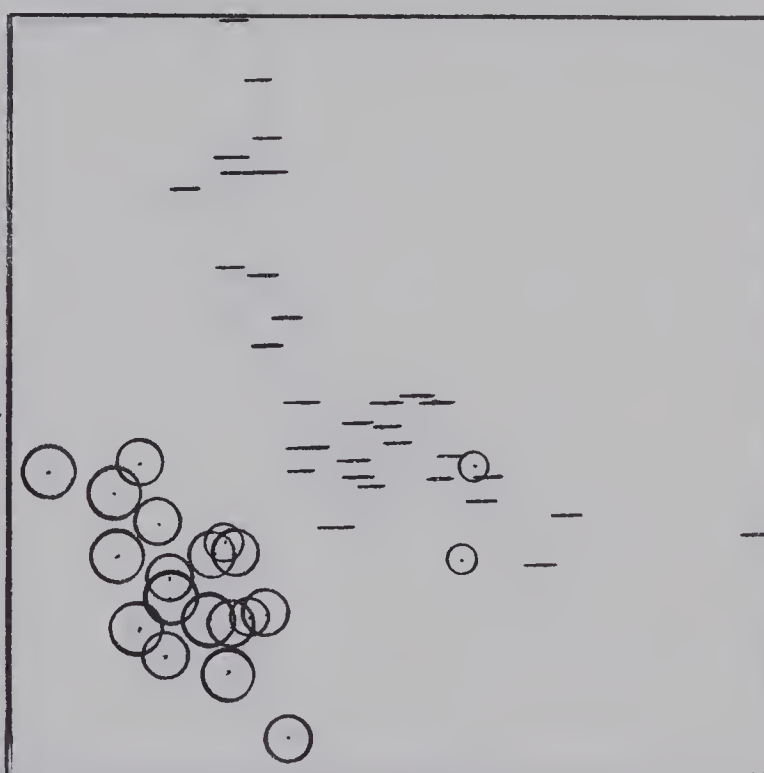
Y



X

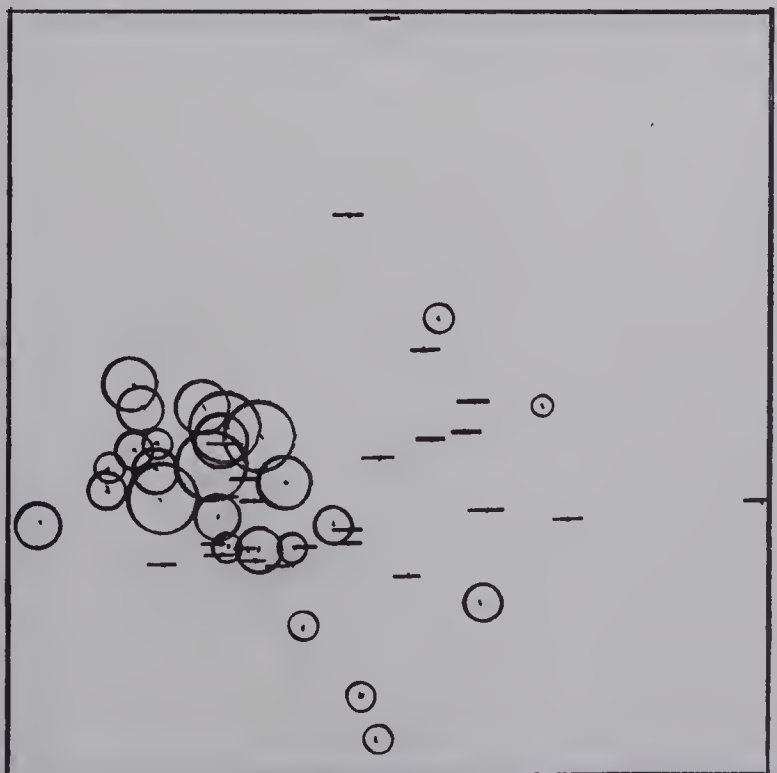
FESTUCA IDAHOENSIS

Z



X

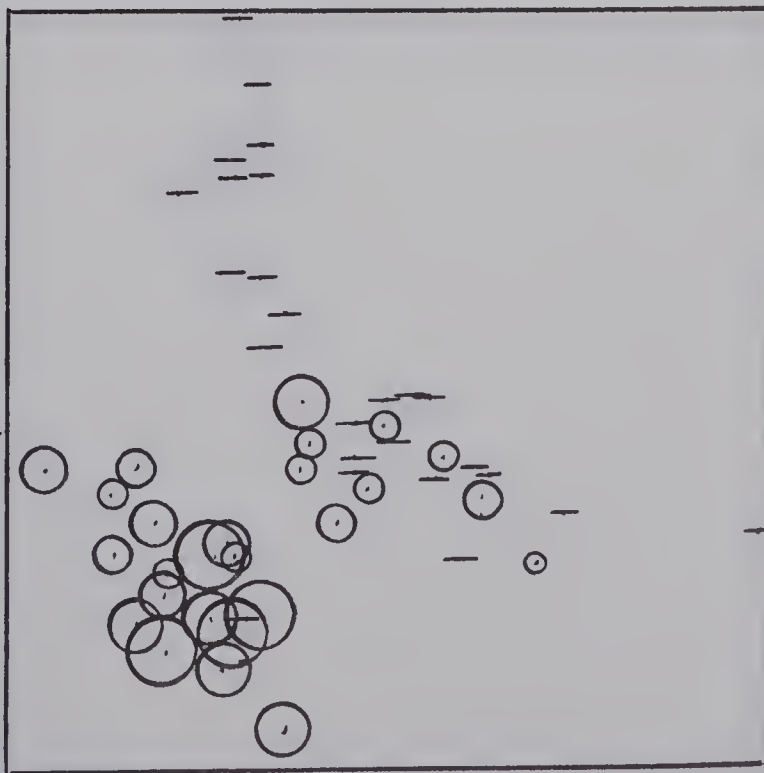
Y



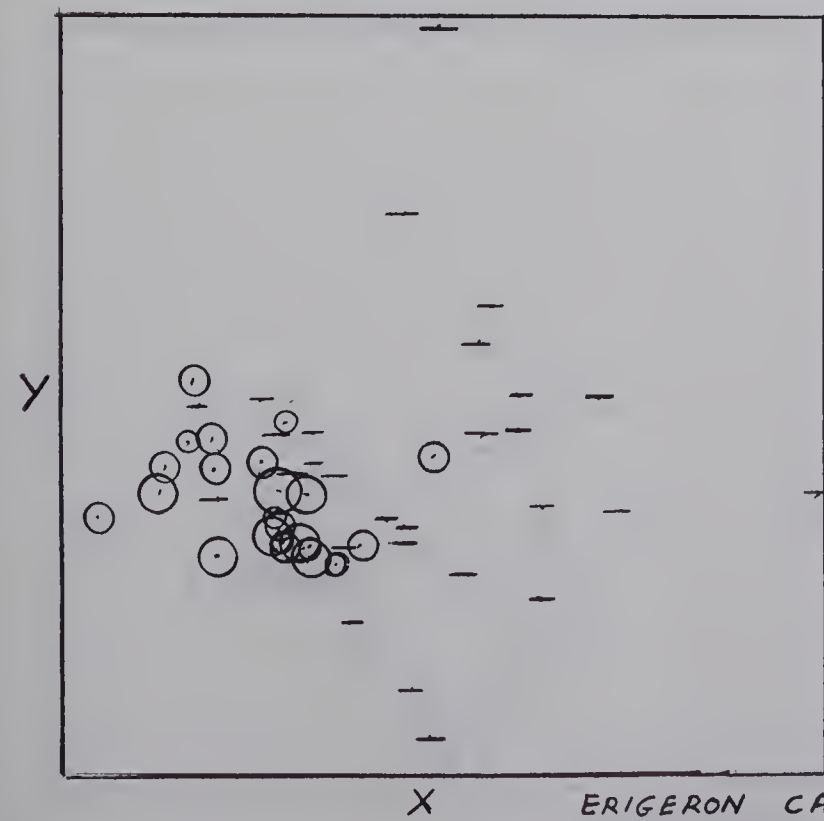
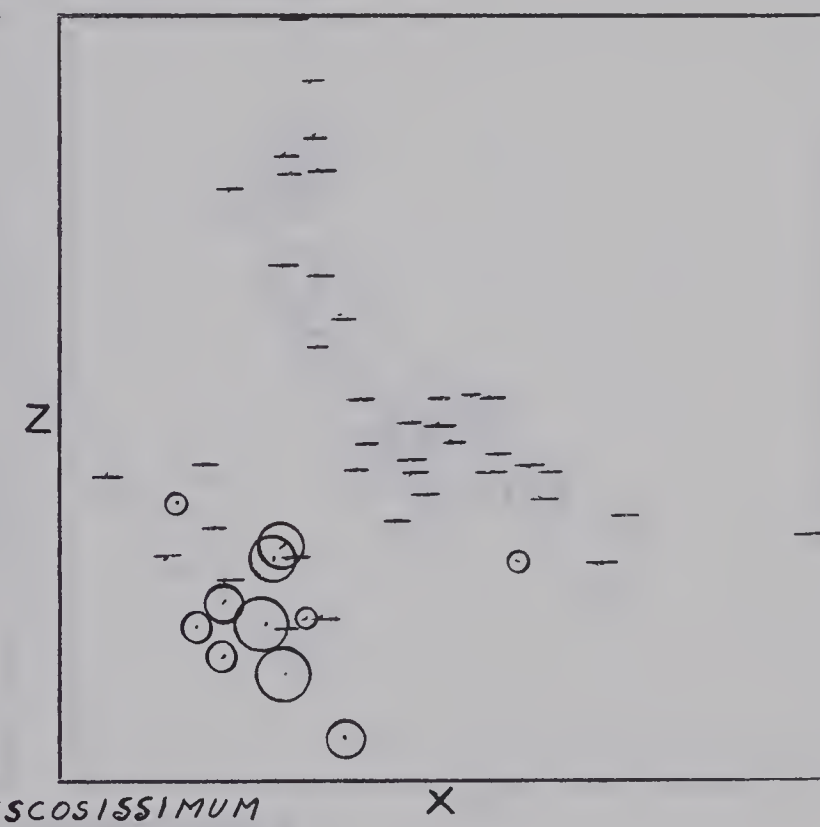
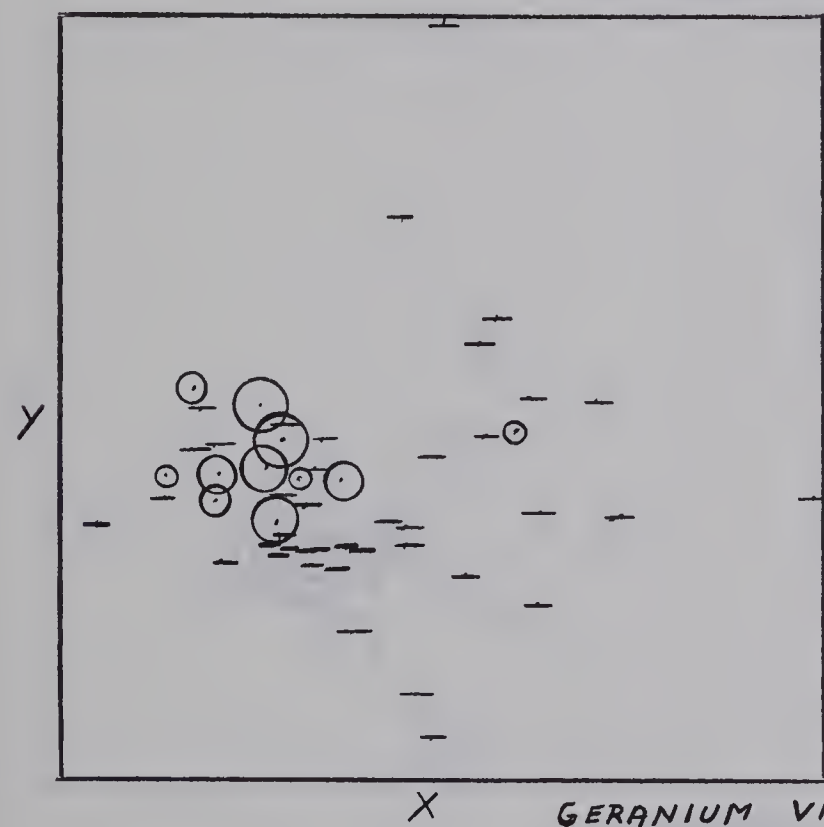
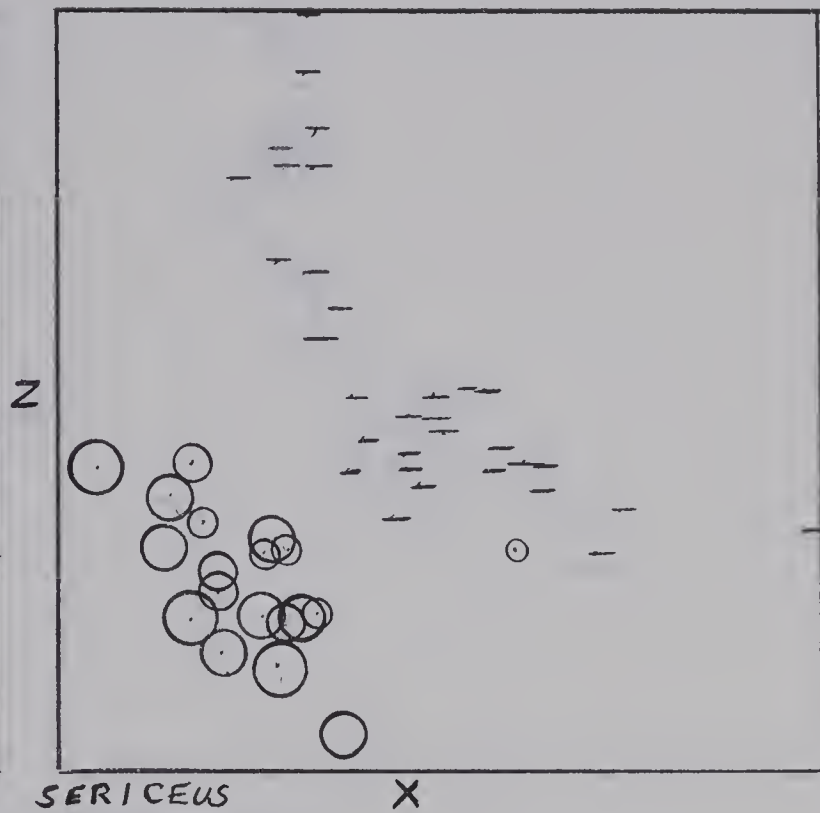
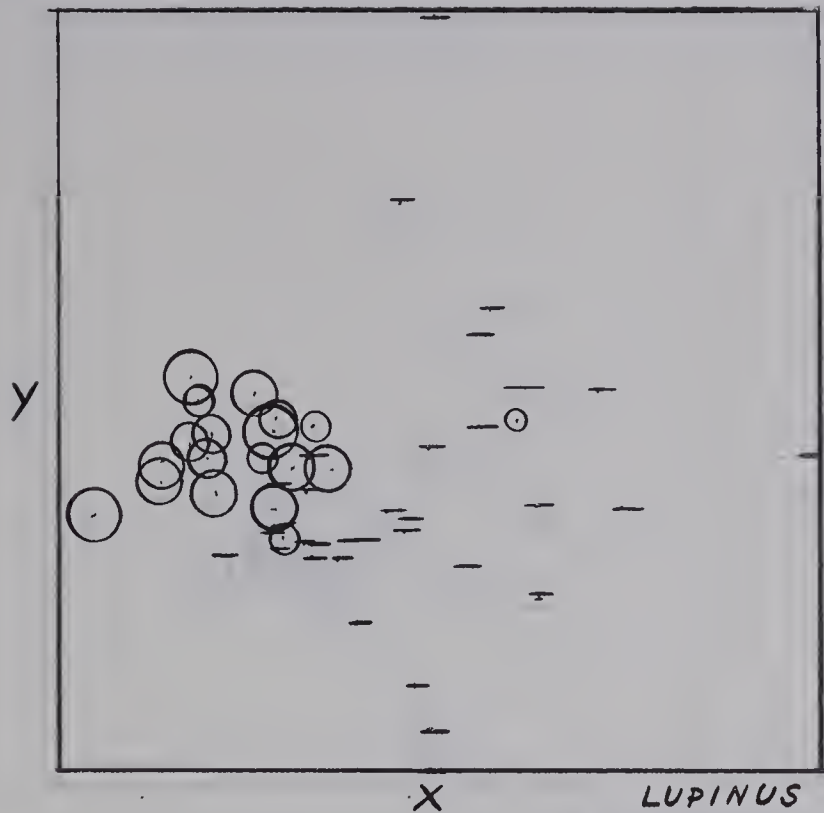
X

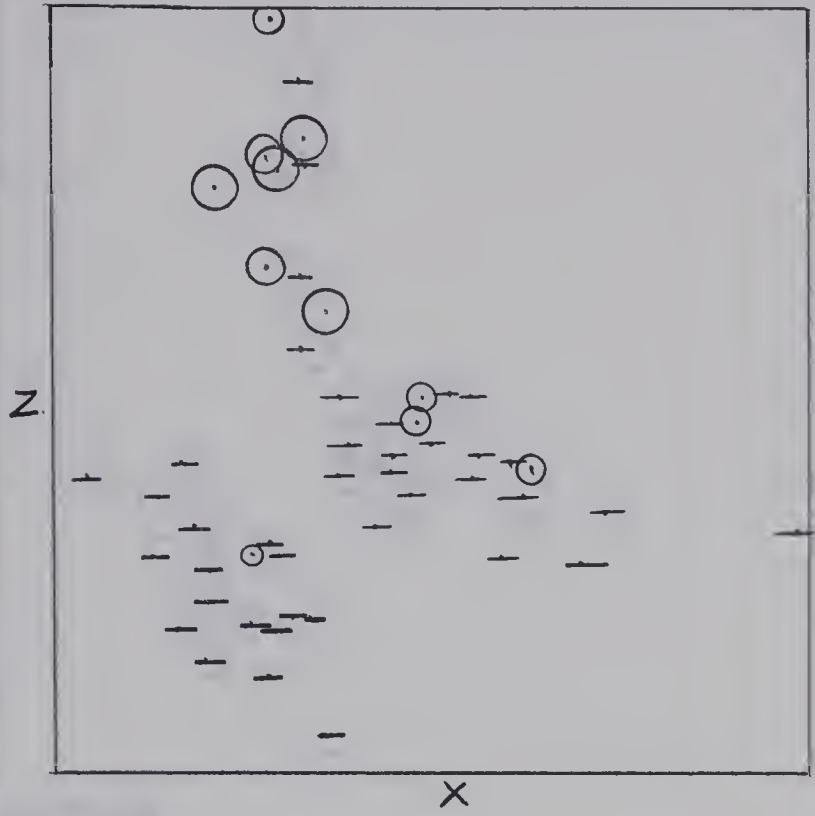
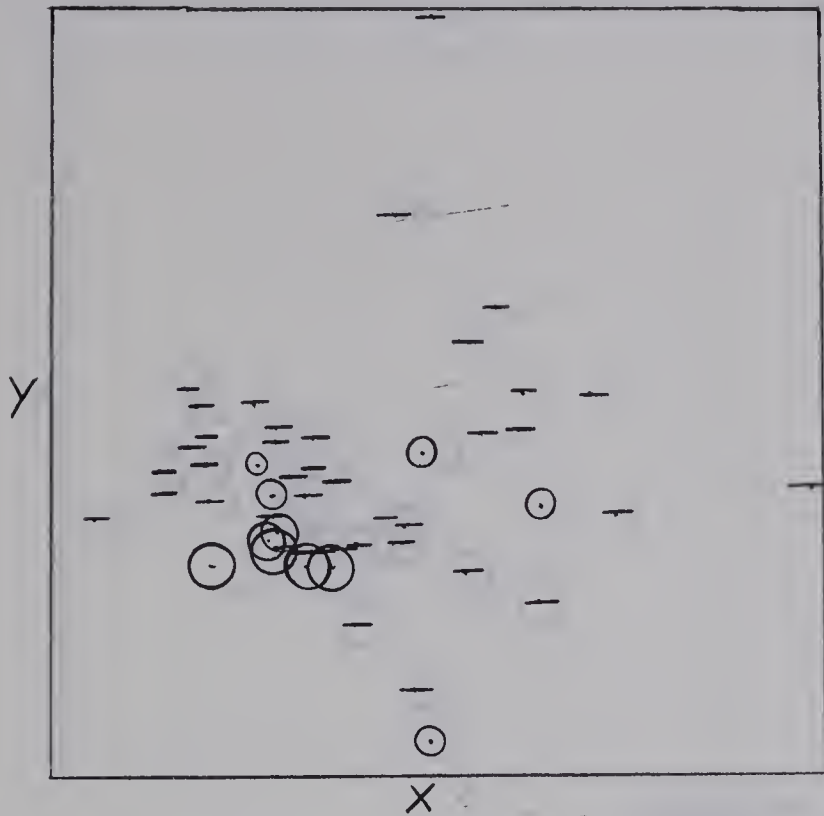
FESTUCA SCABRELLA

Z

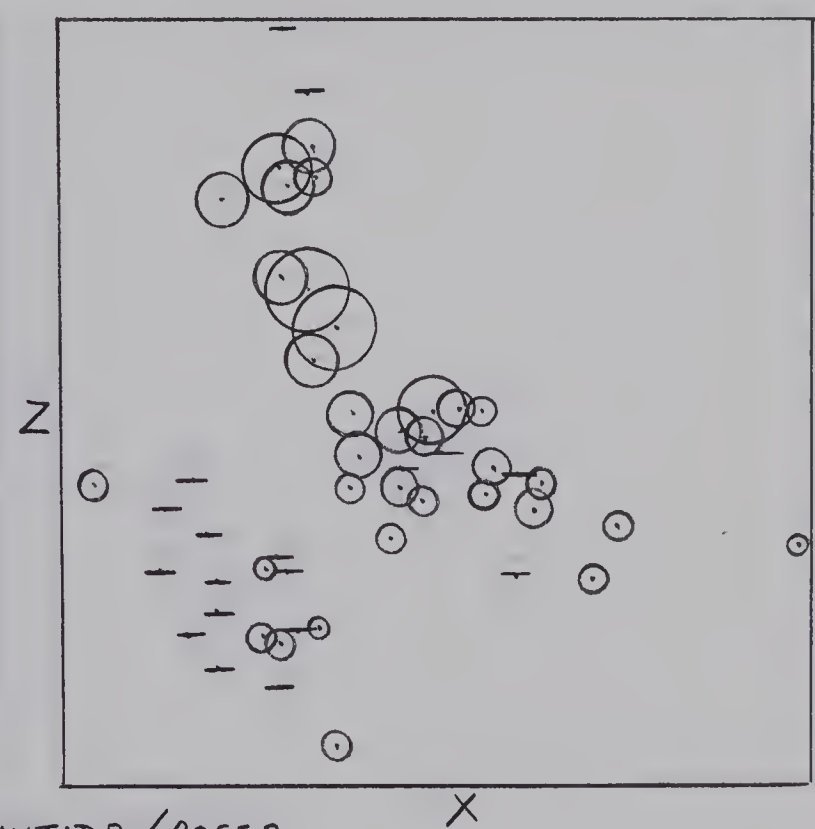
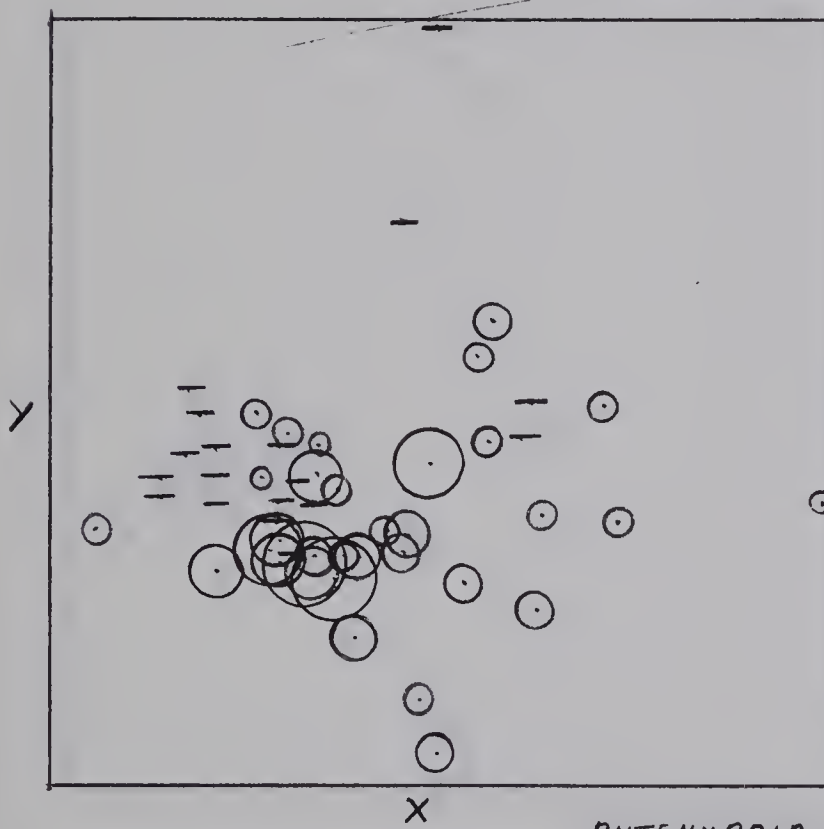


X

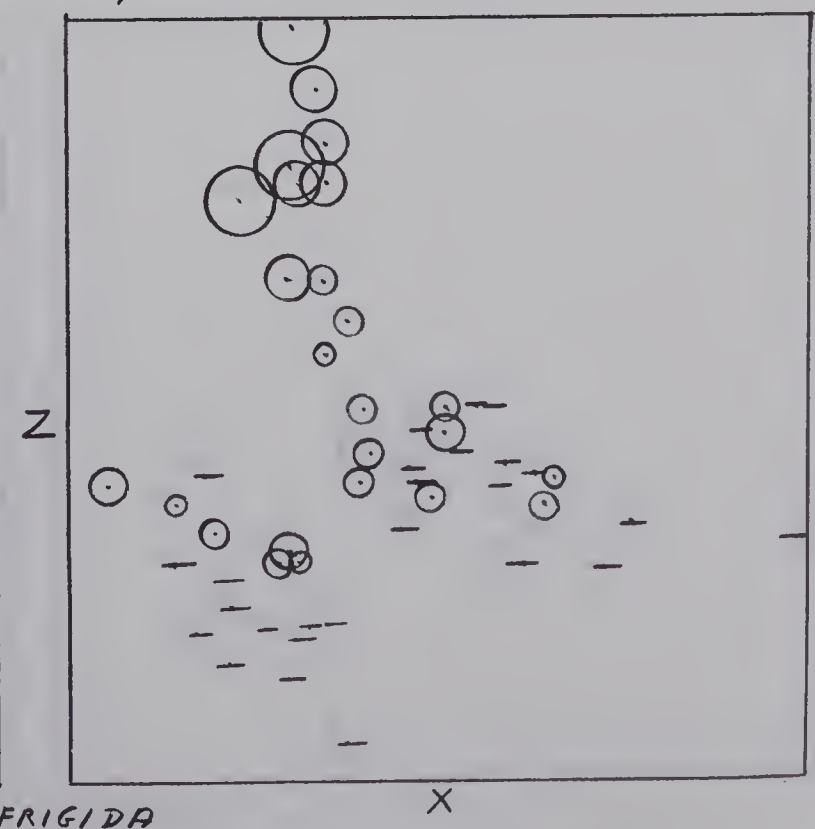
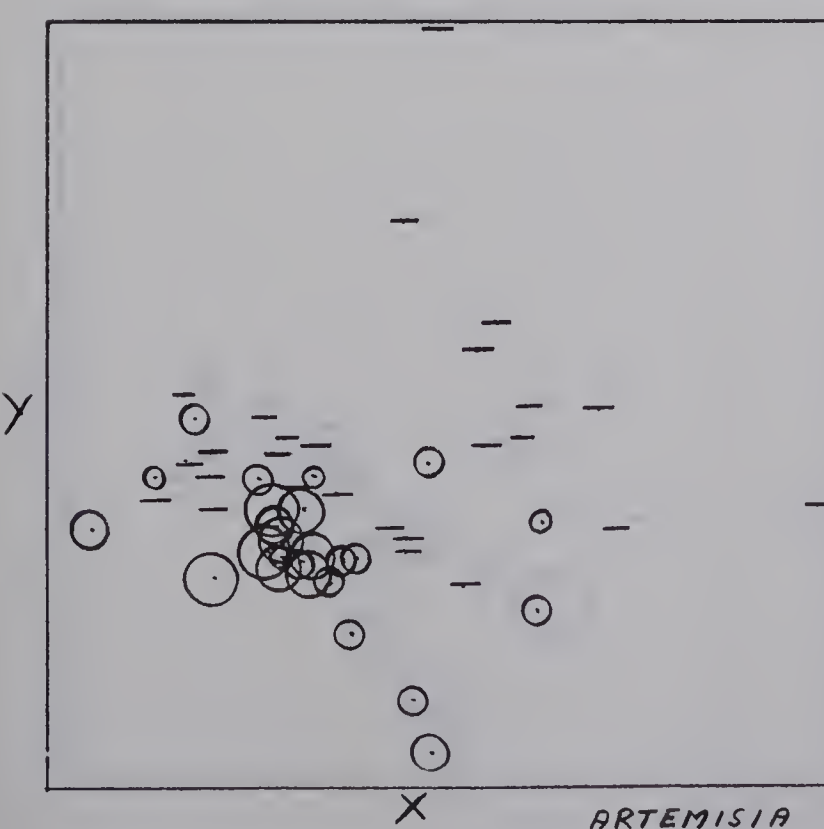




CALAMAGROSTIS MONTANENSIS



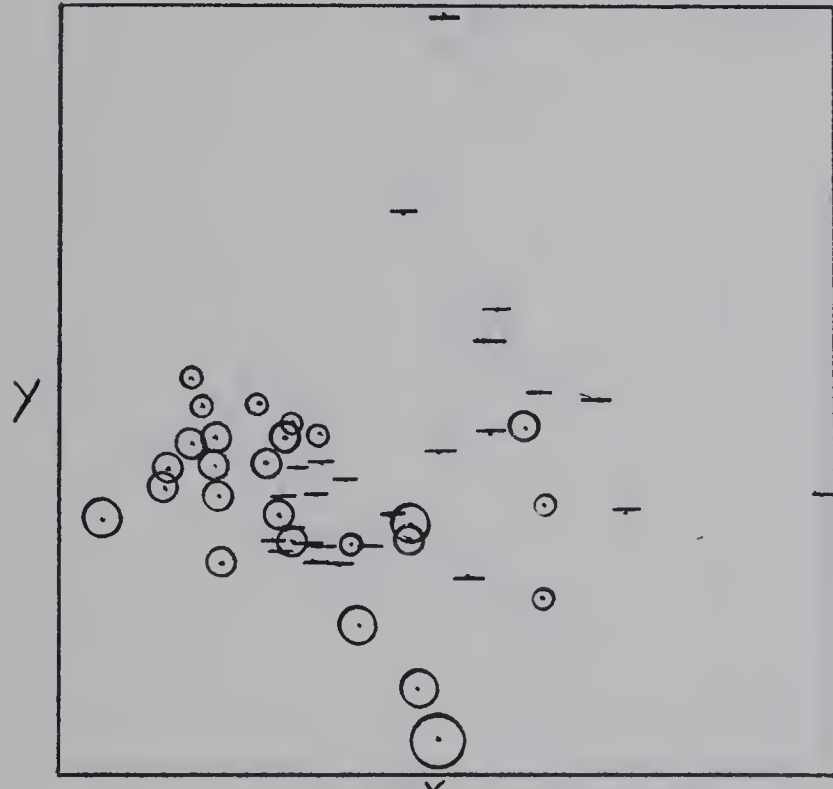
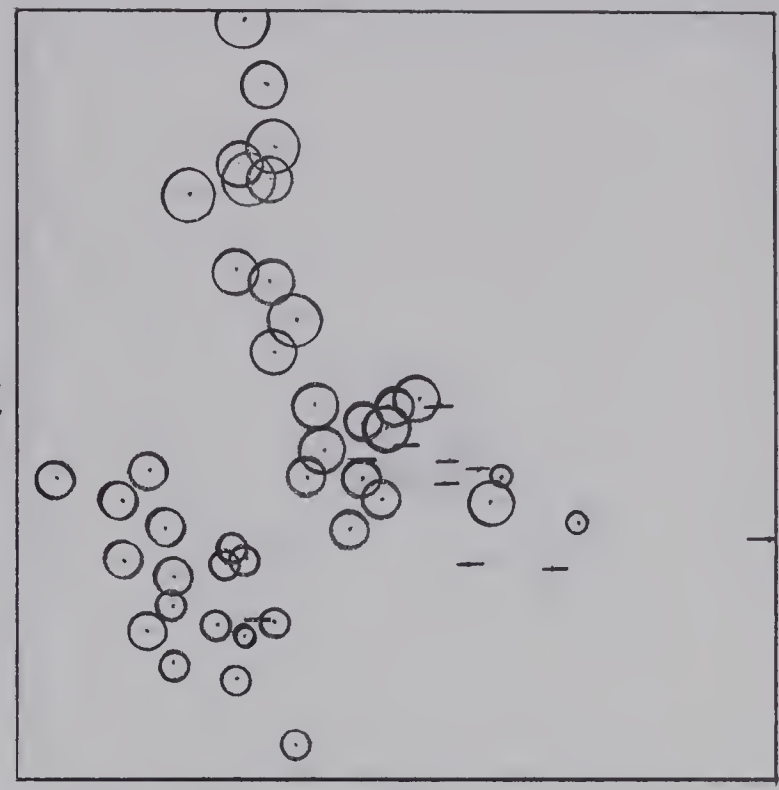
ANTENNARIA NITIDA / ROSEA



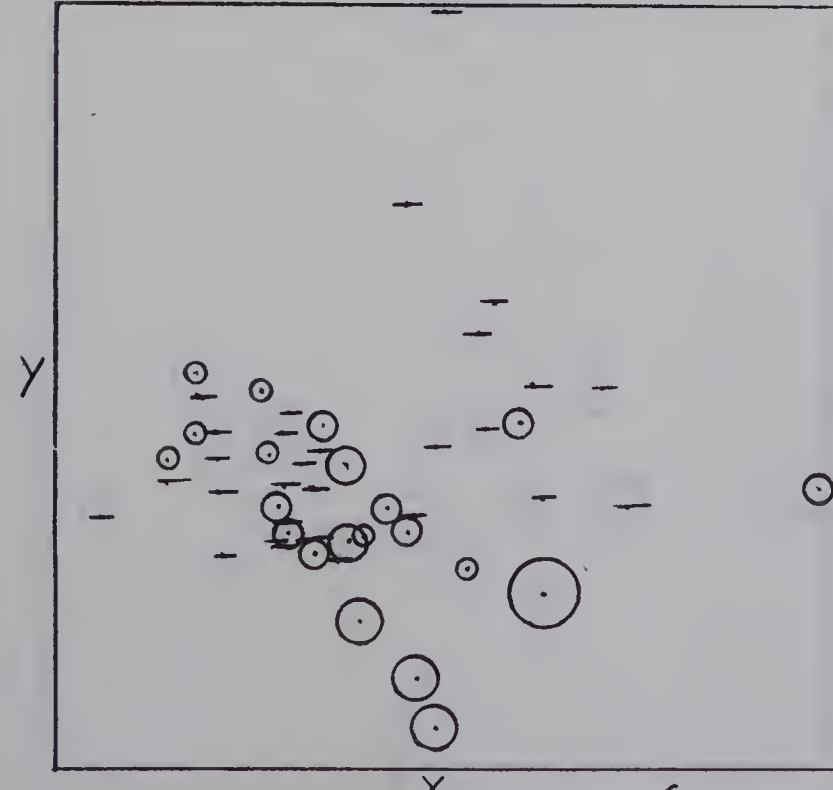
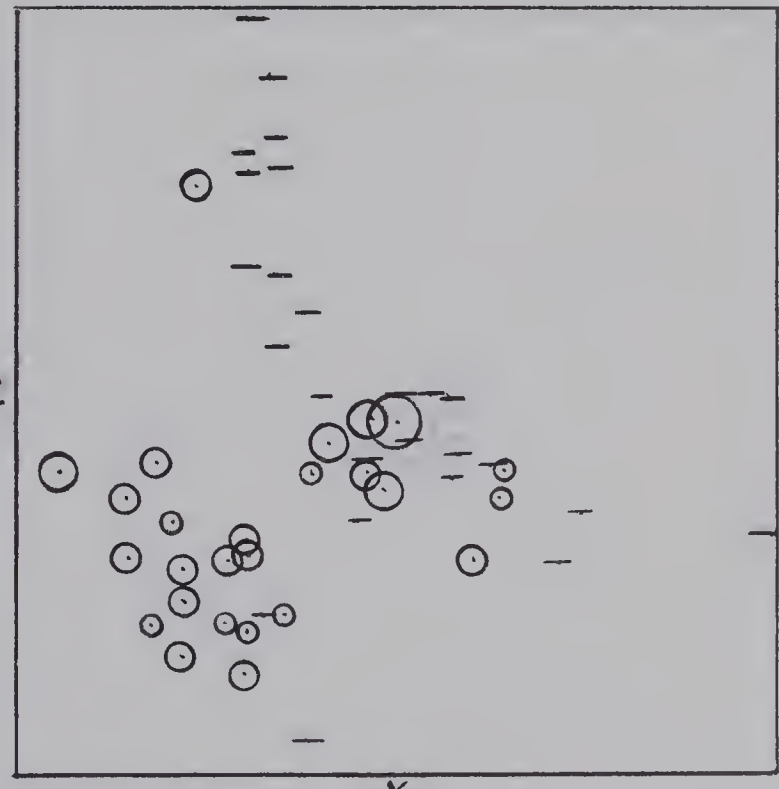
ARTEMISIA FRIGIDA



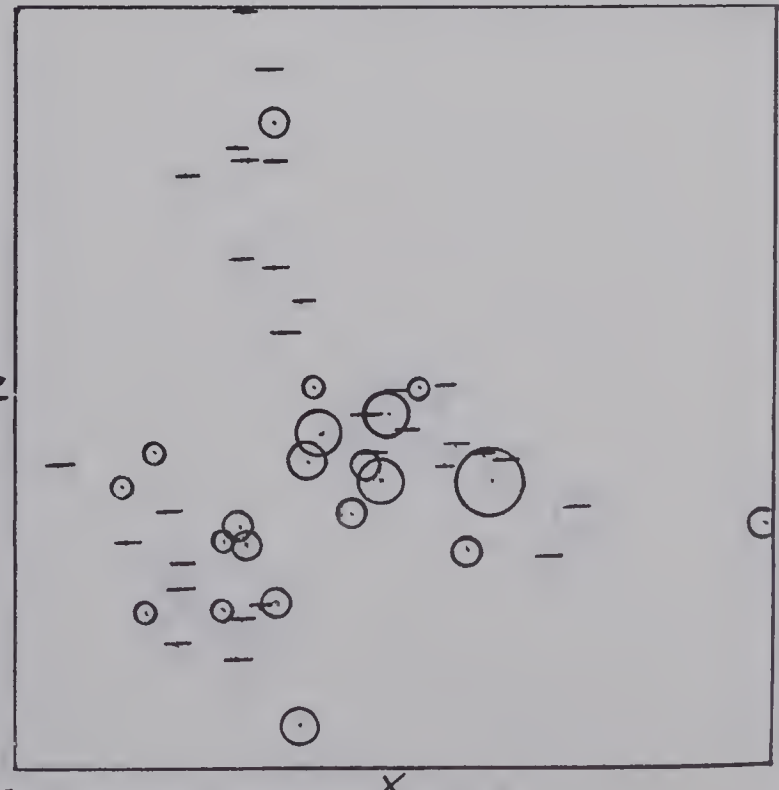
KOELERIA CRISTATA

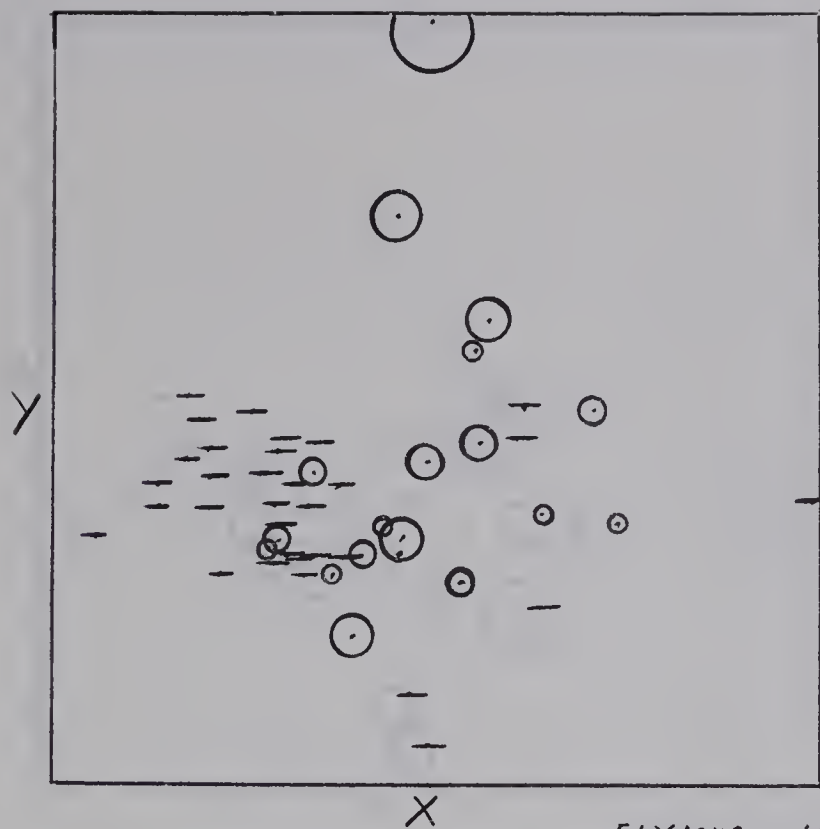
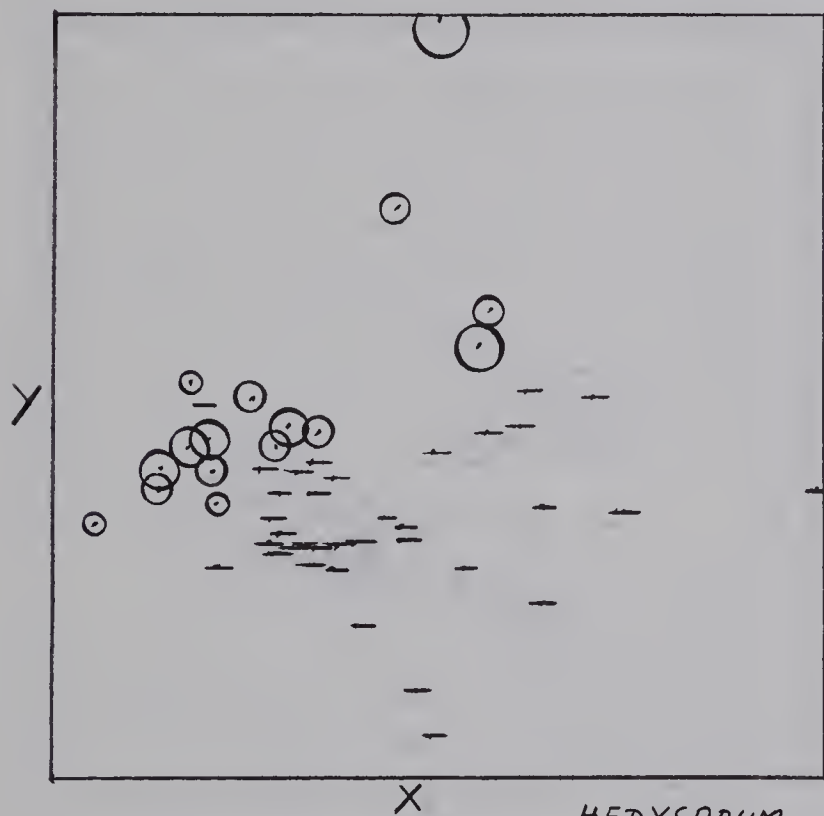
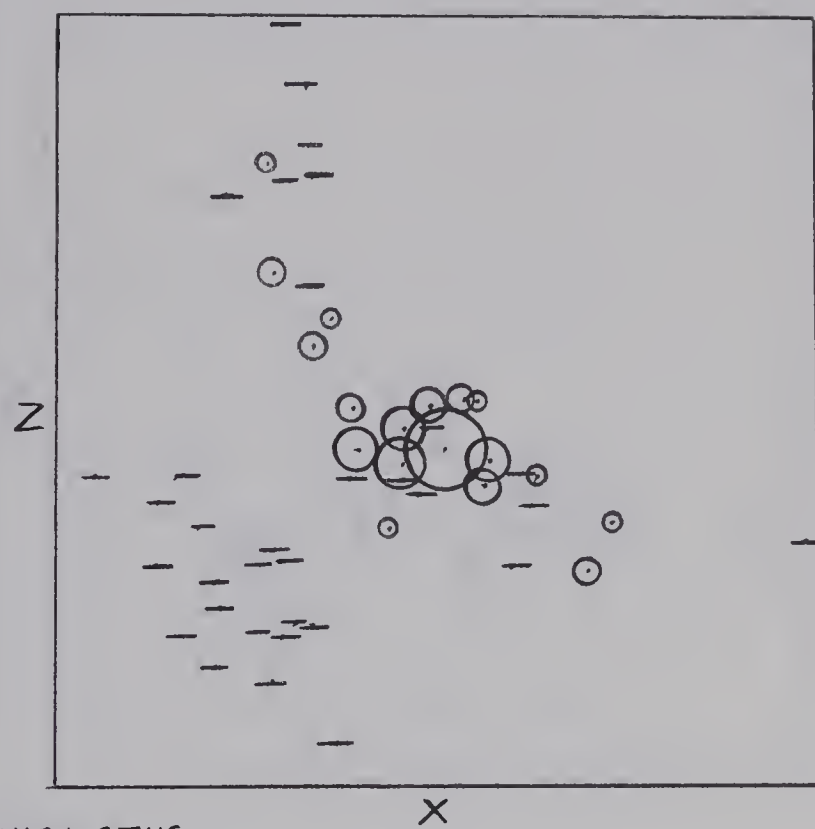
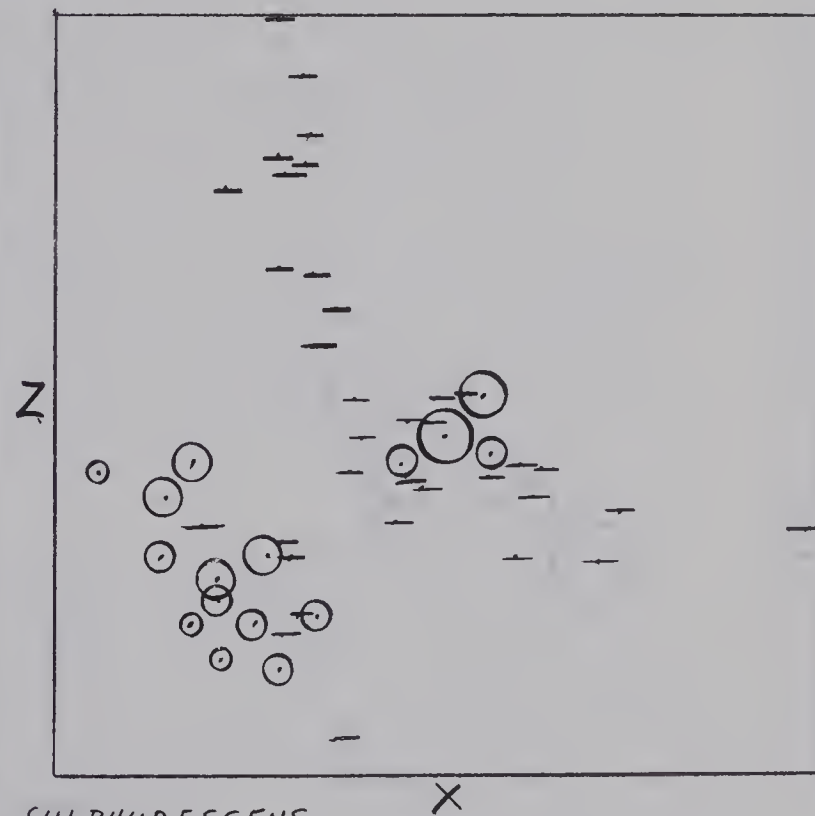
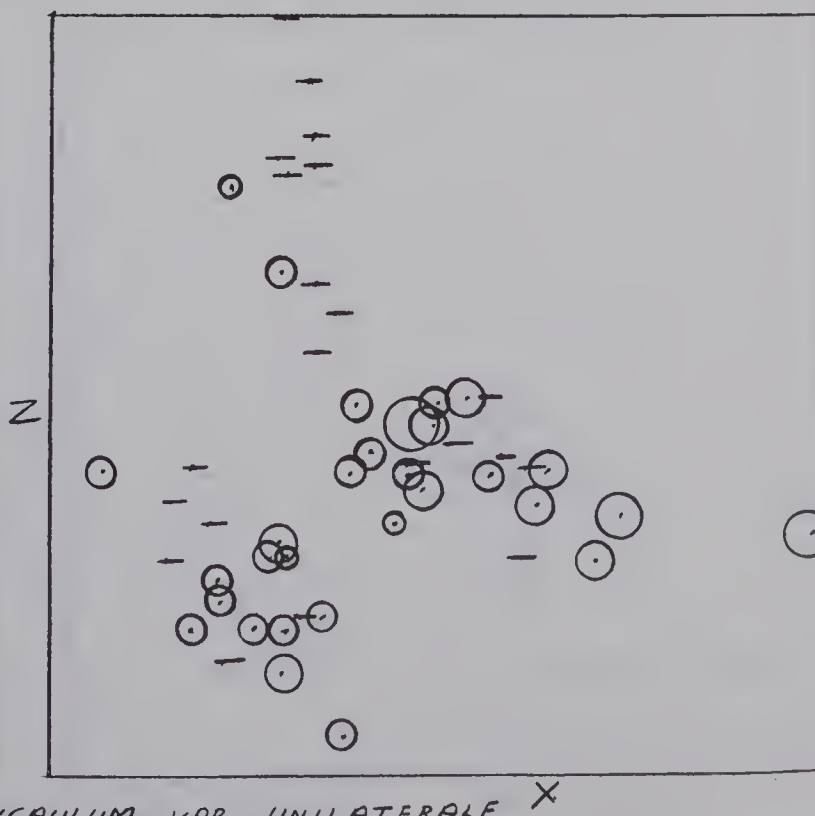


HELICTOTRICHON HOOKERI

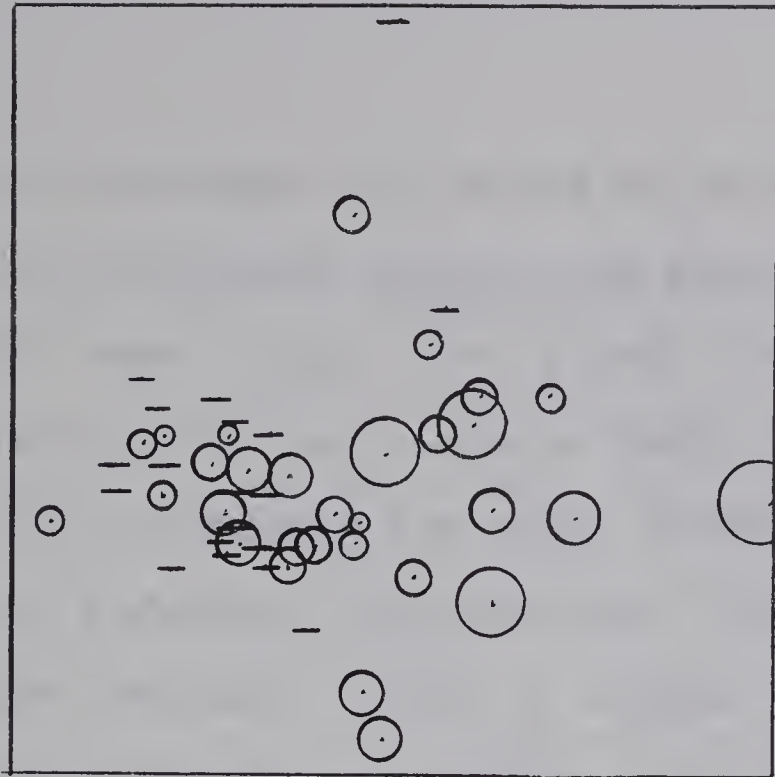


GEUM TRIFLORUM



*ELYMUS INNOVATUS**HEDYSARUM**SULPHURESCENS**AGROPYRON TRACHYCAULUM VAR. UNILATERALE*

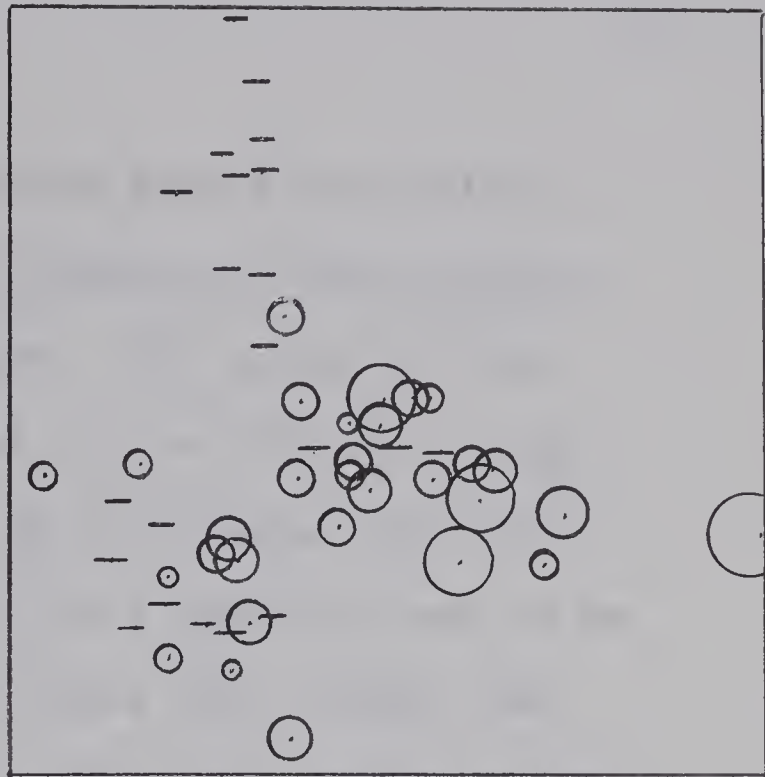
Y



X

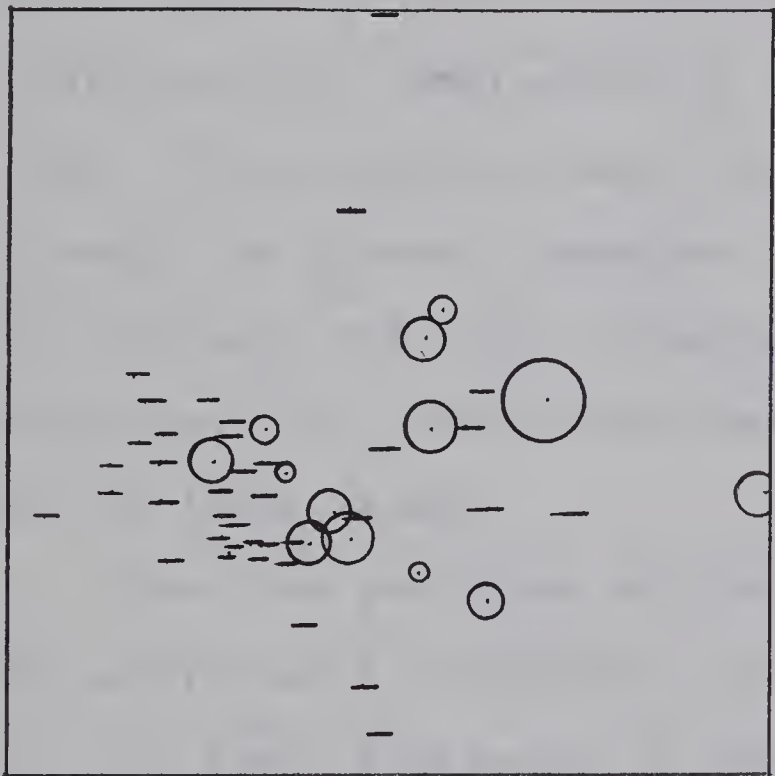
POA PRATENSIS

Z



X

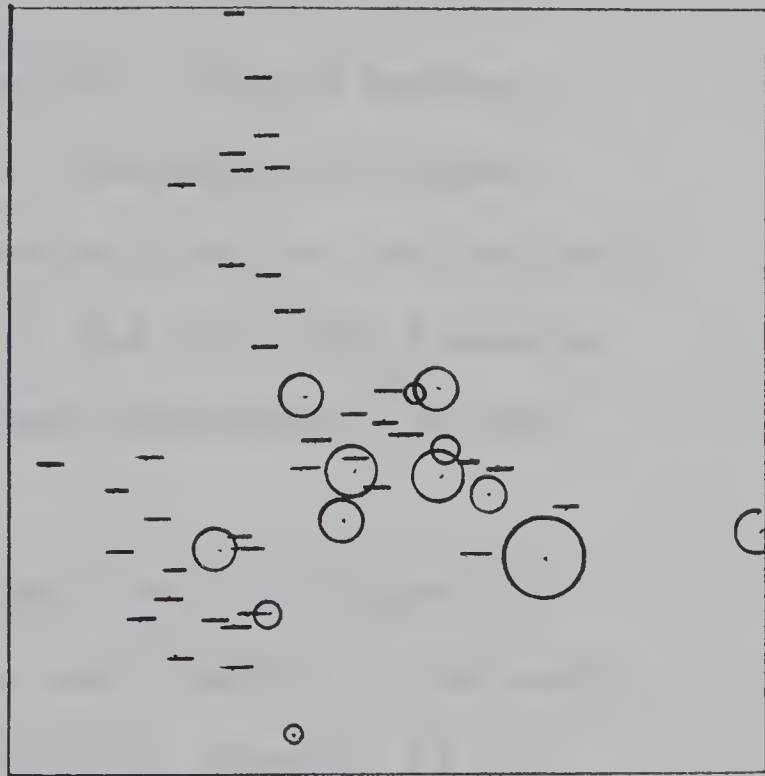
Y



X

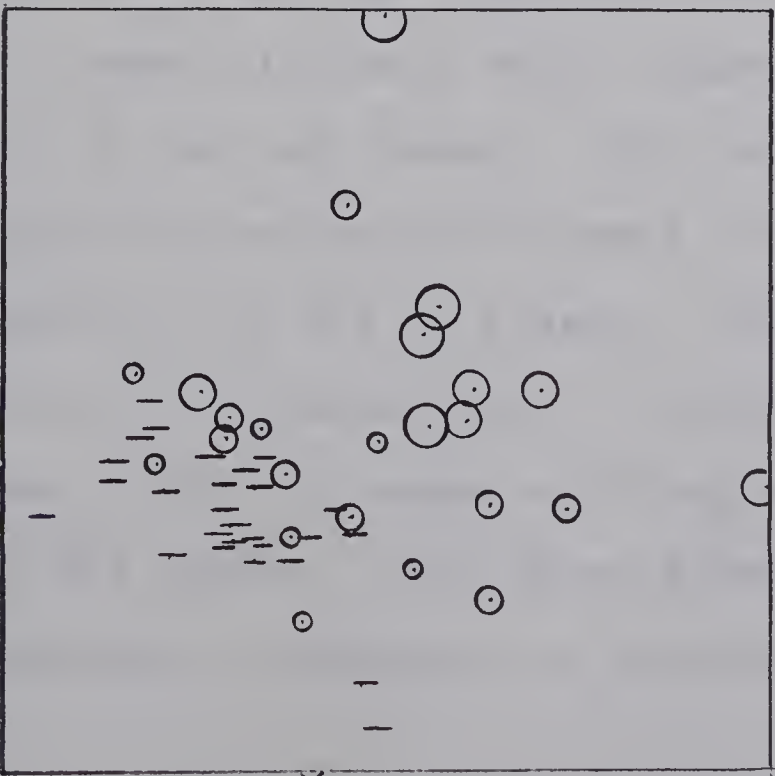
STIPA RICHARDSONII

Z



X

Y



X

FRAGARIA VIRGINIANA VAR. *GLAUCA*

Z



X

In stand Nos. 21, 30 and 31 in the Red Deer River valley, *Helictotrichon hookeri* and *Geum triflorum* are more prominent than in any other stands studied. The group of four high-elevation stands in Banff (Nos. 23 to 26) has a high Cover-abundance for total shrubs and for *Elymus innovatus* and *Hedysarum sulphurescens*. Many other species tend to be more abundant in one or another of these four groups and it is therefore possible to extract lists of species which, taken together, would characterize each of them (*i.e.*, "characteristic combination of species", Braun-Blanquet, 1932). This cannot be done for the remaining 15 stands, although the grasses *Agropyron trachycaulum* var. *unilaterale*, *Poa pratensis* and *Stipa richardsonii* and the forb *Fragaria virginiana* var. *glauca* have their peak abundances in certain of these stands.

Since the positions of the stands on the ordination are determined by similarity to the end stands of the axes, *i.e.*, by their similarity to only 6 of 51 stands, it is possible that some centrally-placed stands will have little in common with each other except their dissimilarity to all six of the end stands. This patterning occurred on the grassland ordination because of the great vegetational diversity of the 51 stands. For example, when the species lists are scrutinised, it is apparent that Nos. 9 and 10 have little in common with any of the stands close to them in the centre. This three-dimensional ordination is, therefore, inadequate to elucidate and portray the vegetational

relationships of some of the centrally-placed stands.

Patterns of Environmental Variables on the Ordination

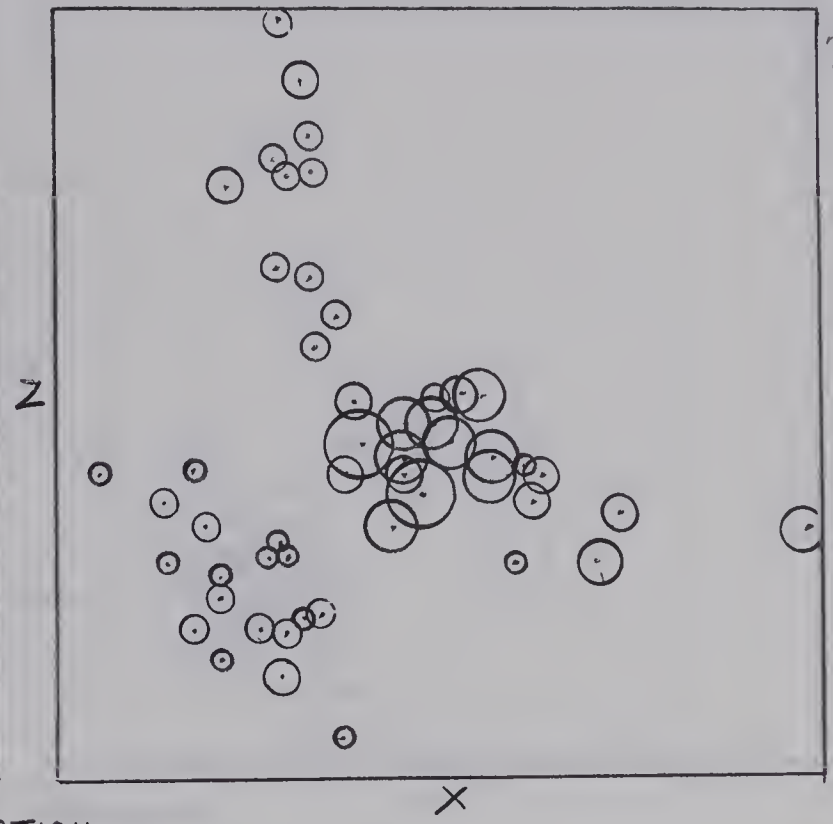
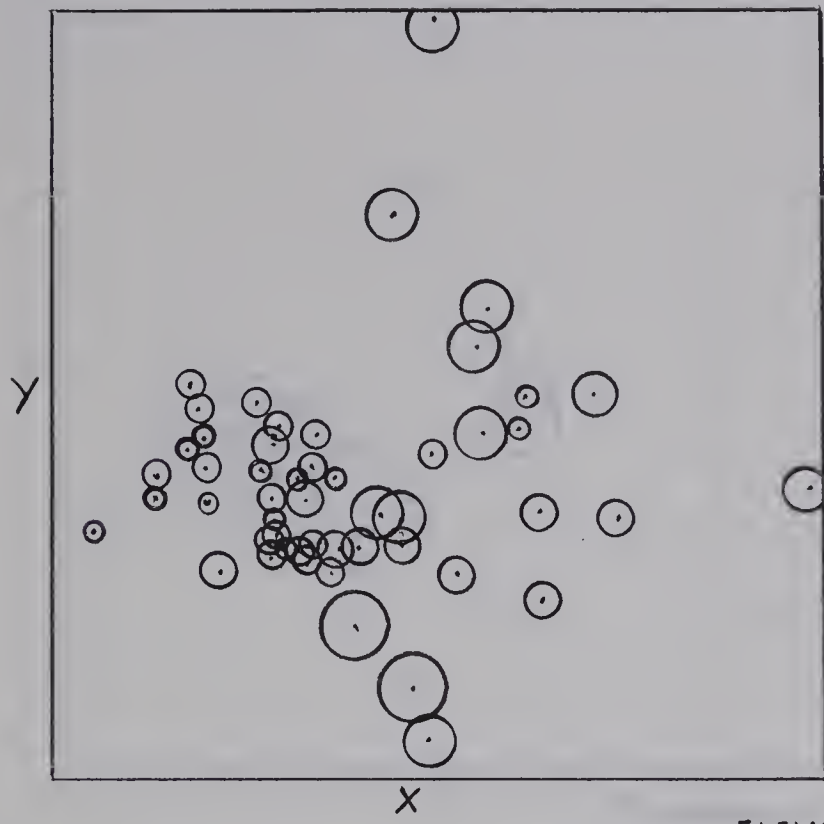
By plotting the distribution of environmental variables on the ordination field as circles of different sizes, correlations with vegetational attributes or species distribution can be detected. Stand values for the following were plotted: available nitrogen, phosphorus and potassium, pH, percentage gravel, sand and clay, Permanent Wilting Percentage, Field Capacity and Water Availability of the soil at several depths; thickness of the A horizon; grazing activity; mean elevation, slope angle and aspect; penetrometer readings of surface compaction. A number of the more meaningful patterns may be seen in Fig. 12.

Available nitrogen at 3 inches (8 cm) depth was very low or nil in most stands, *i.e.*, less than 5 ppm at the time of sampling, and in only Nos. 9 and 10 at Waterton did this nutrient seem not to be limiting. Available phosphorus at 3 inches (8 cm) depth was also very low in most stands, especially the more xeric stands in the Red Deer River valley and arid Jasper groups and some stands central on the ordination. This nutrient was evidently less limiting in many of the main Waterton group and the high elevation group.

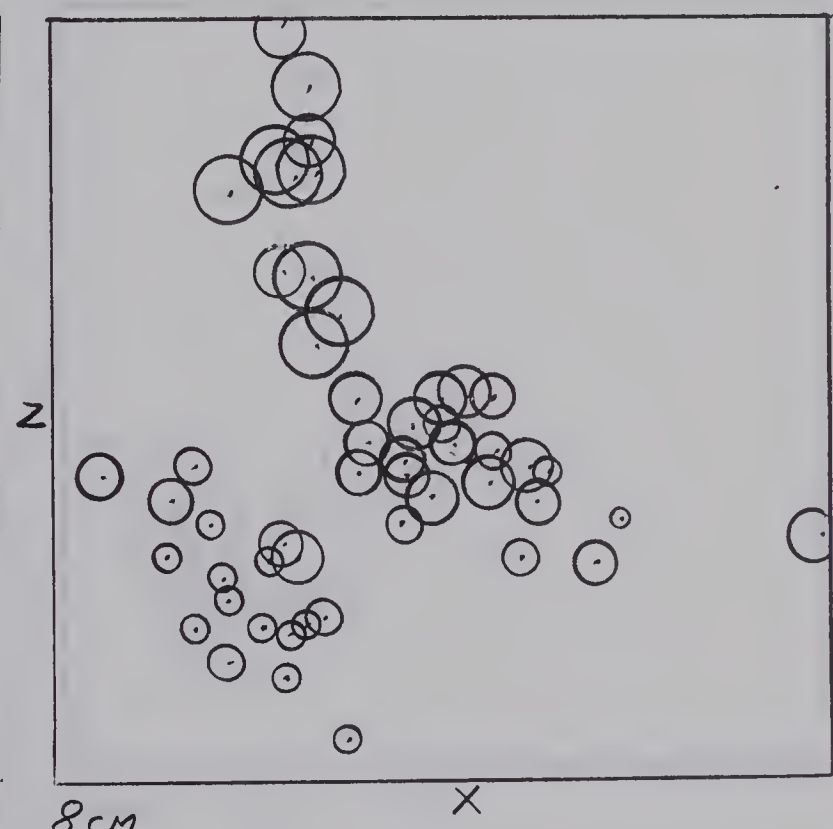
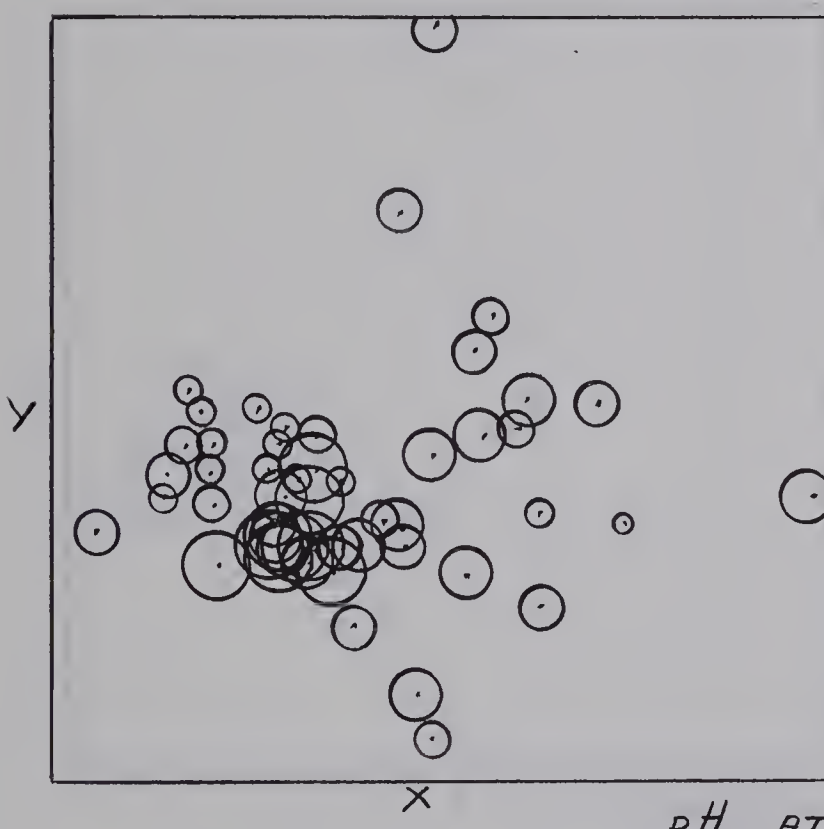
Available potassium at 8 cm was lowest in the arid Jasper group and highest in the main Waterton group.

Figure 12. The distribution patterns of nine environmental variables on the XY and XZ planes of the 51-stand ordination.

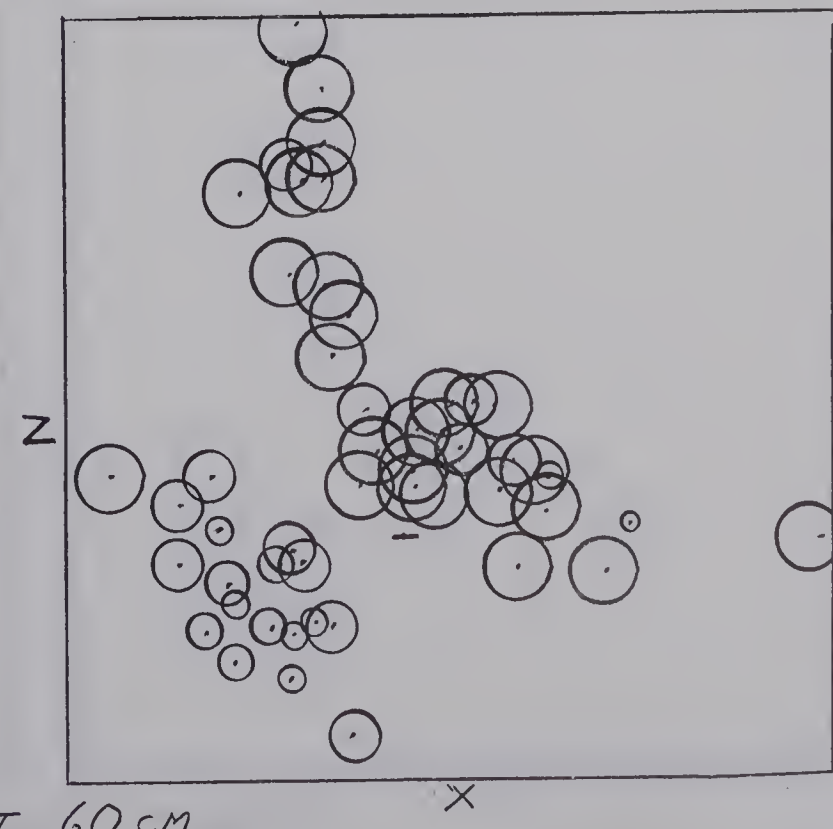
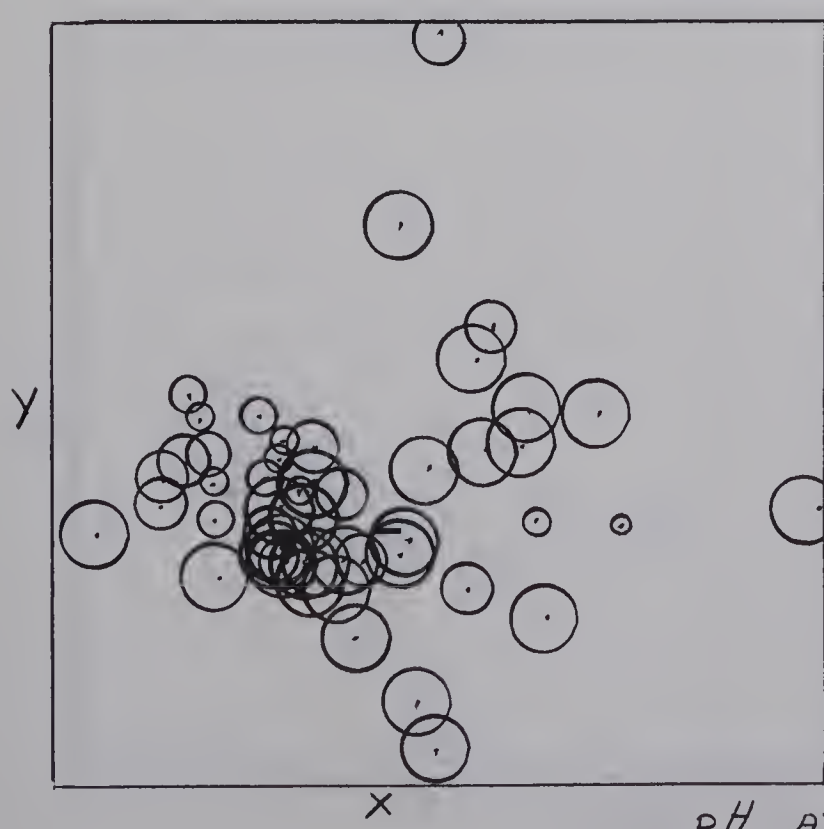
- A. Elevation, compensated for latitude: progressively larger circles represent classes of 4,000-4,495, 4,500-4,995, 5,000-5,495, 5,500-5,995, 6,000-6,495, and 6,500-7,000 ft.
- B. pH at 8 cm: progressively larger circles represent classes of less than 6.0, 6.0-6.4, 6.5-6.9, 7.0-7.4, 7.5-7.9, and 8.0 and over.
- C. pH at 60 cm: progressively larger circles represent the same values as "B".
- D. A horizon thickness: progressively larger circles represent classes of 0-4, 5-9, 10-14, 15-19, 20-24, and 25 cm and over.
- E. Sand/clay ratio: progressively larger circles represent classes of 0-5, 5-10, 10-15, 15-20, 20-25, and 25-30.
- F. Total grazing intensity: progressively larger circles represent classes of pellet groups 0-9, 10-19, 20-39, 40-59, 60-99, and 100 and over in 1,800 ft². (167 m²).
- G. Gravel %, weighted mean to 90 cm: progressively larger circles represent classes of 0-9.9, 10.0-19.9, 20.0-39.9, 40.0-59.9, 60.0-79.9, and 80.0-100.0%.
- H. Available phosphorus at 8 cm: progressively larger circles represent classes of 0-2, 2½-4½, 5-7, 7½-9½, 10-12, and over 12, in ppm.
- I. Available potassium at 8 cm: progressively larger circles represent classes of less than 50, 50-99, 100-149, 150-199, 200-249, and 250 and over, in ppm.



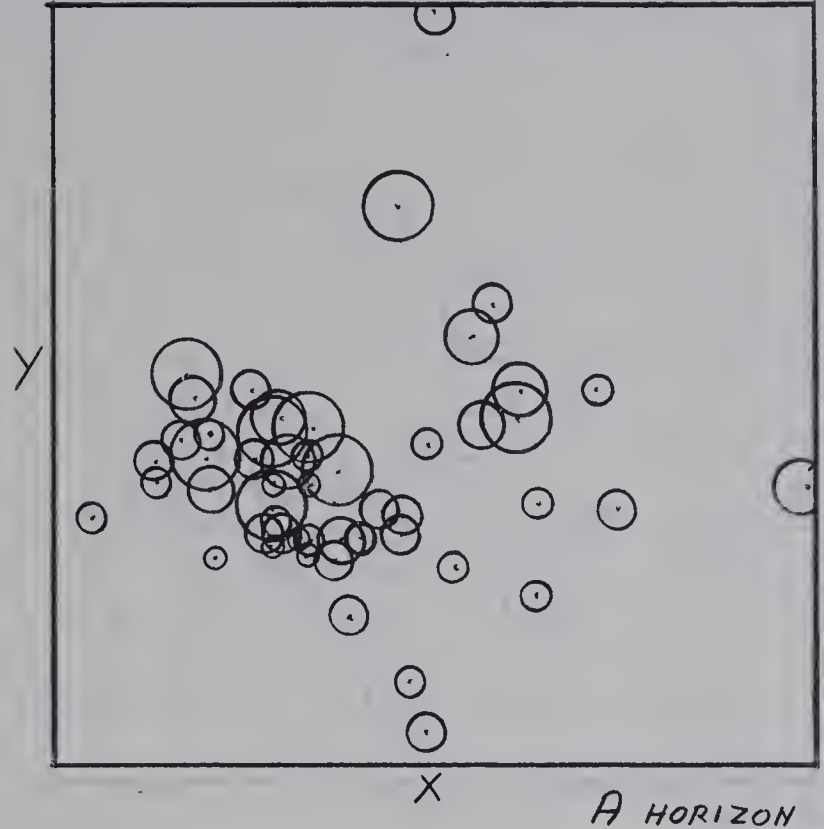
ELEVATION



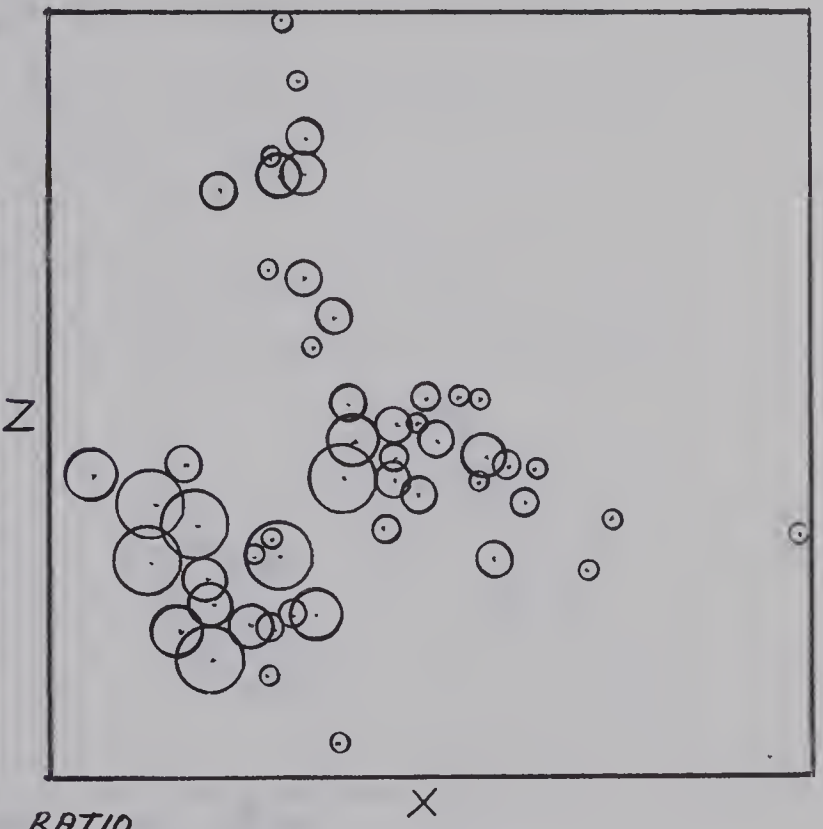
pH AT 8cm



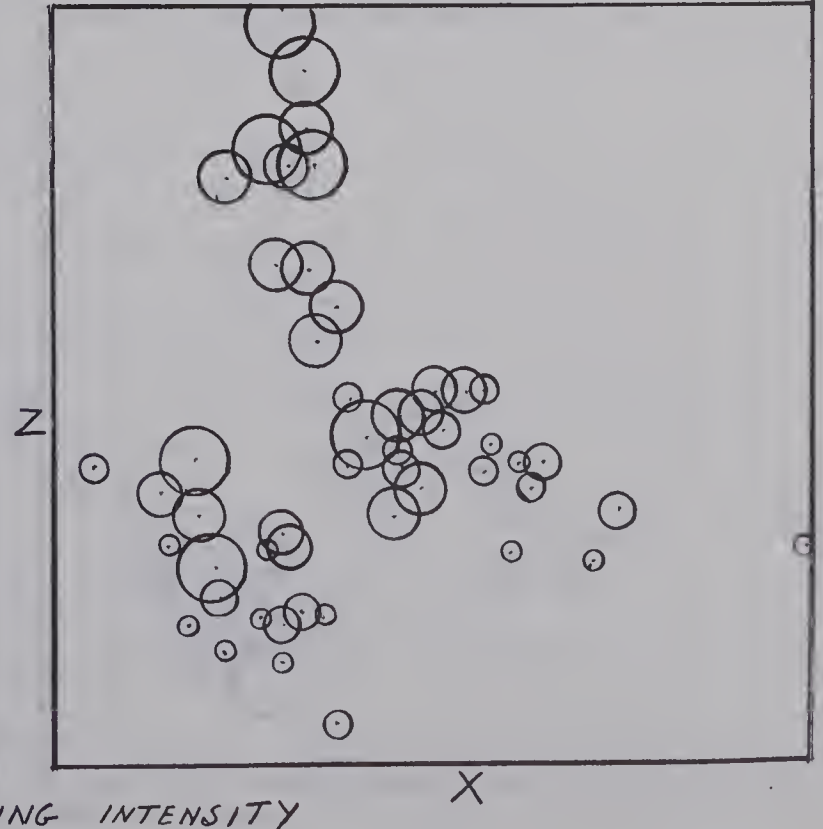
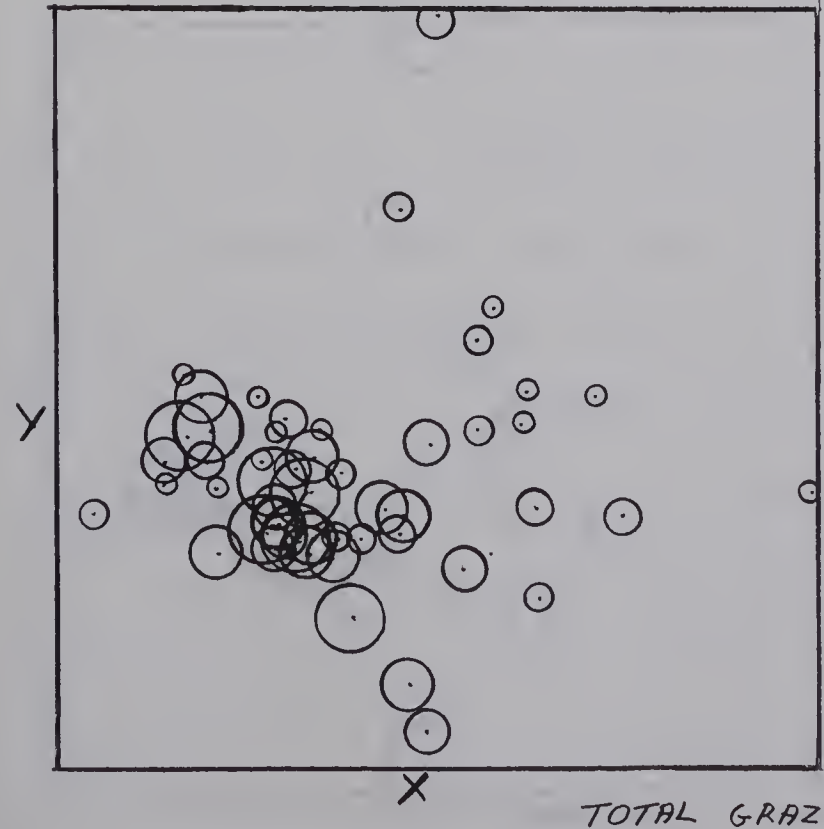
pH AT 60cm



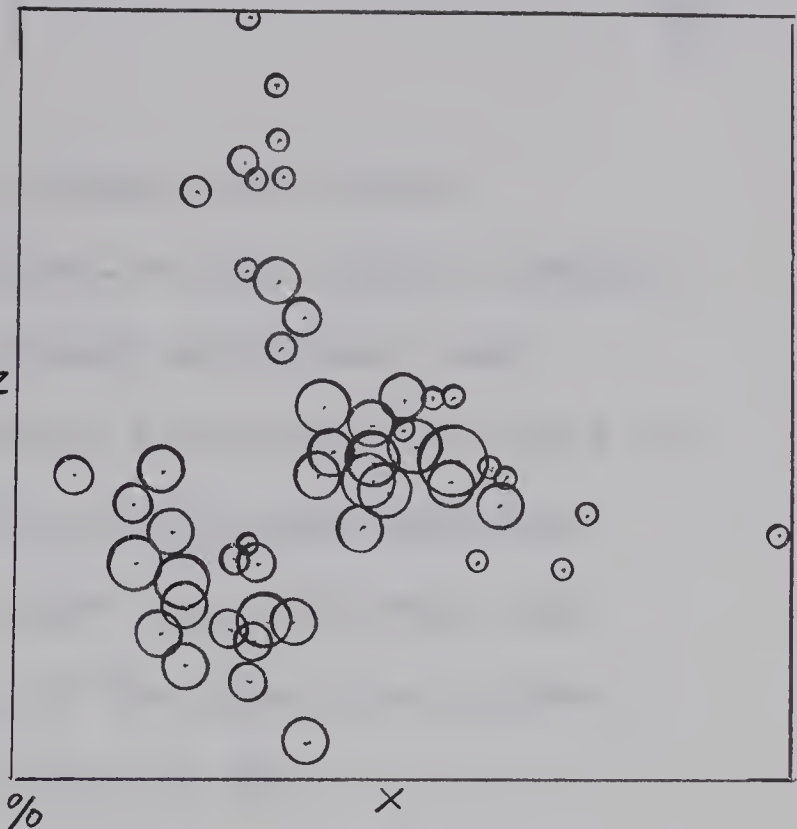
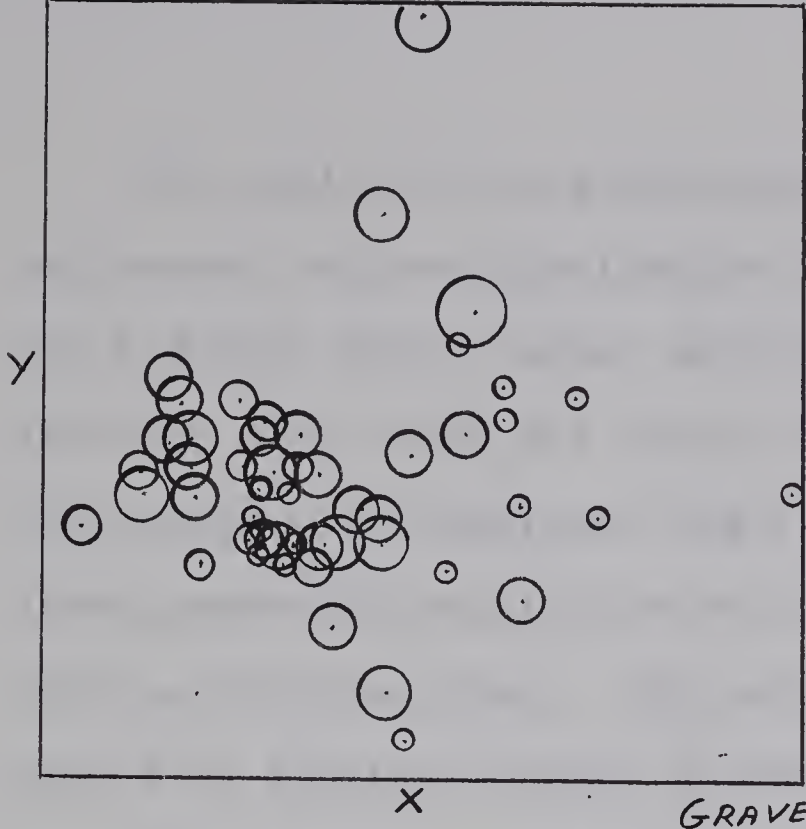
A HORIZON THICKNESS



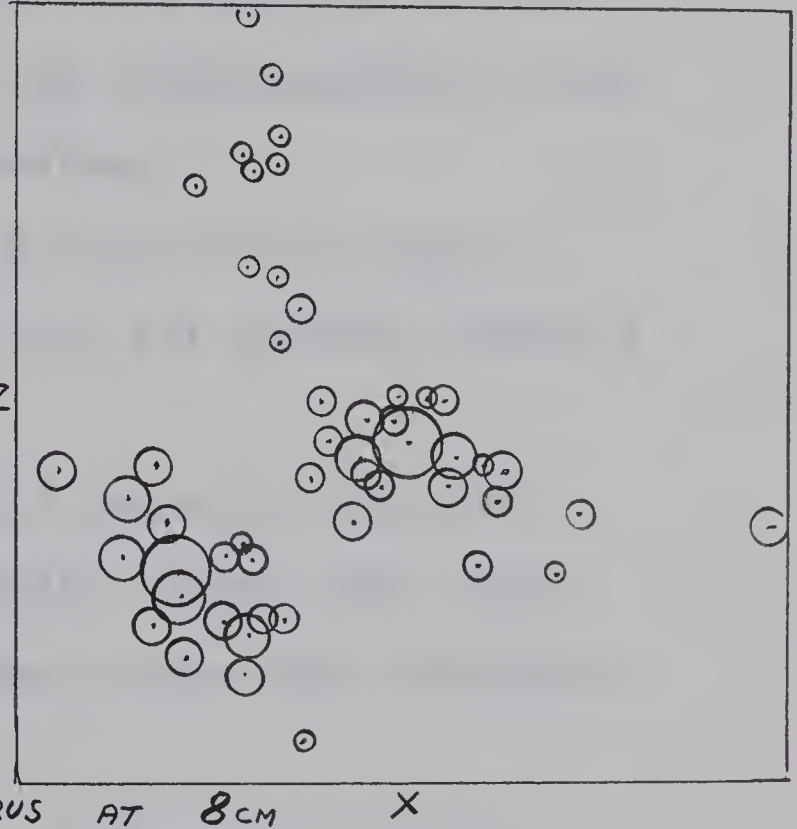
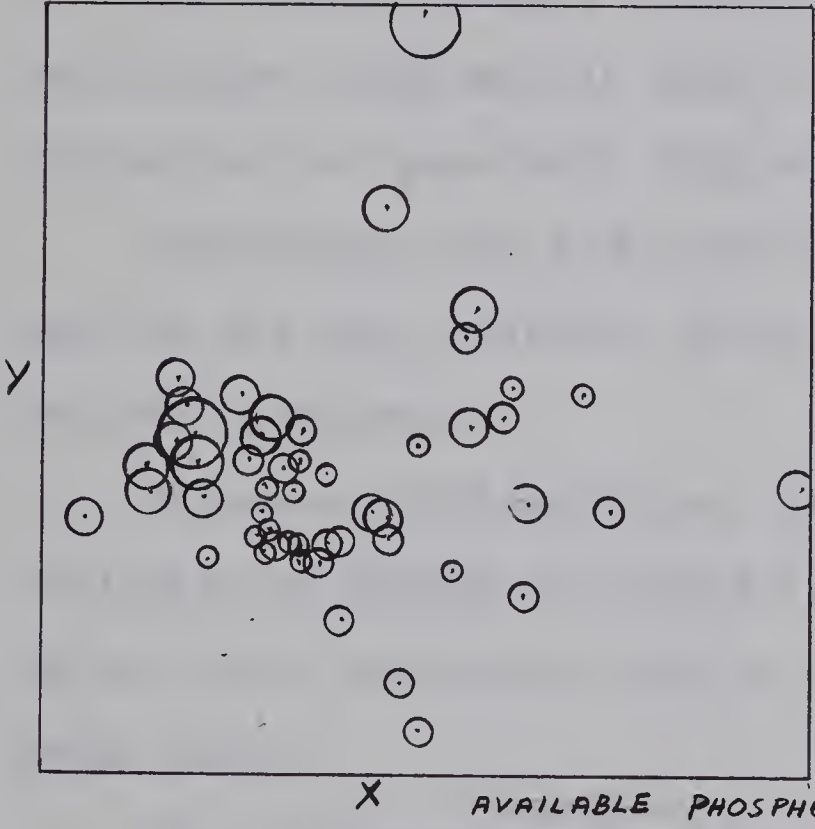
SAND/CLAY RATIO



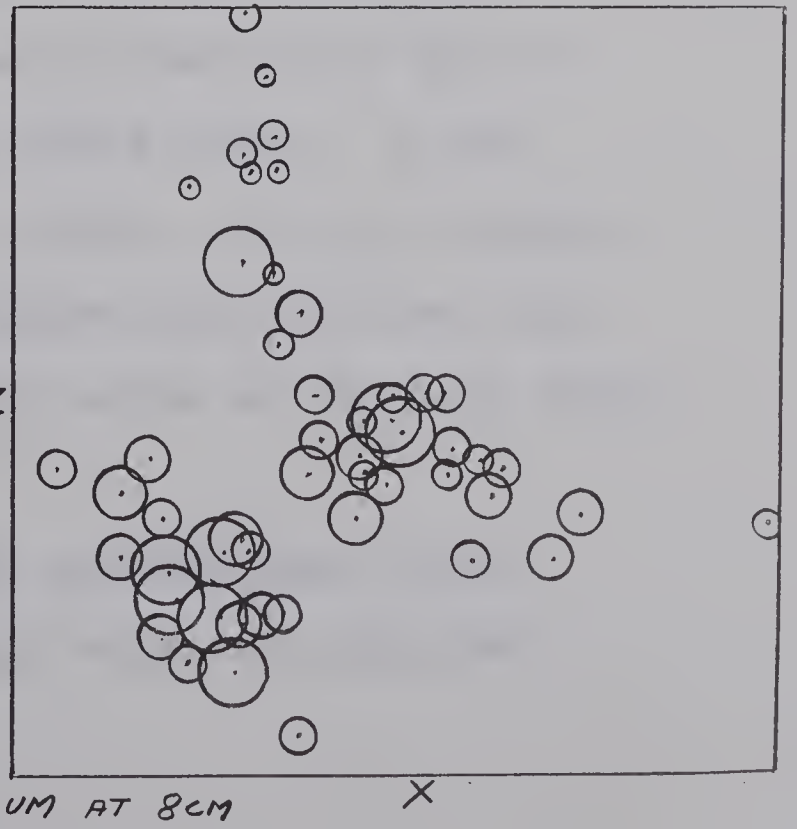
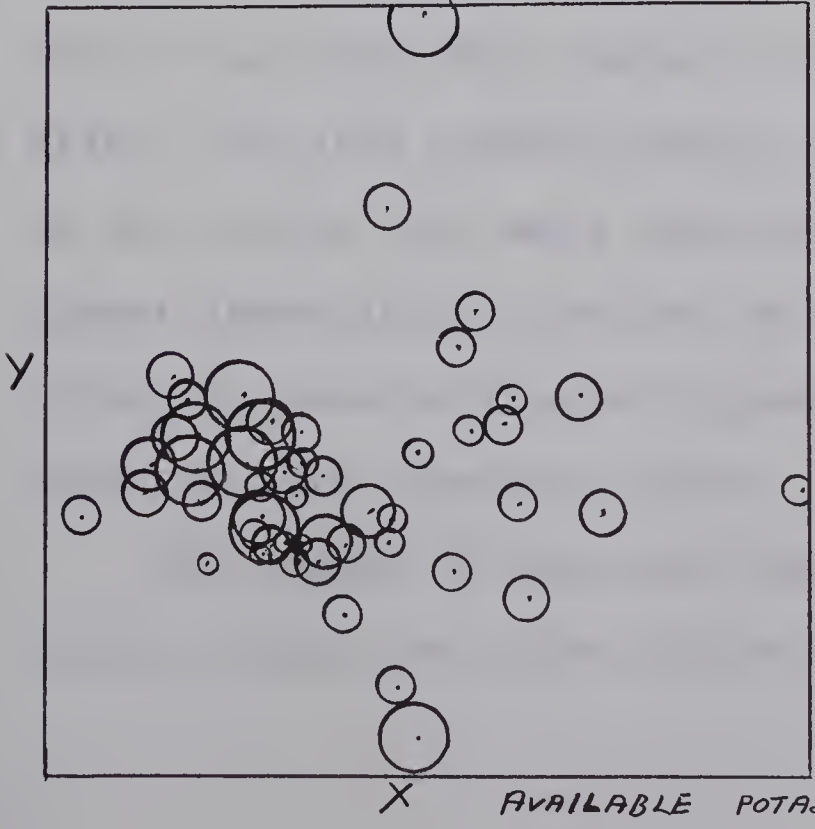
TOTAL GRAZING INTENSITY



GRAVEL %



AVAILABLE PHOSPHORUS AT 8 CM



AVAILABLE POTASSIUM AT 8 CM

The soils of the arid Jasper group were highly calcareous and had alkaline pH values at all depths sampled; the Red Deer River valley soils became calcareous and alkaline with depth and their surface horizons were close to neutral pH. In contrast, the soils of the main Waterton group generally had little or no free lime, and many had acid surface horizons. The soils of the other two groups showed no distinct trends in free lime or pH.

The gravel content of soil profiles was low in the arid Jasper group and in some of the stands central on the ordination but generally high elsewhere.

Percentage sand and sand/clay ratios were high in most of the main Waterton group soils but neither showed a pattern elsewhere.

Permanent Wilting Point, Field Capacity and Water Availability showed no marked trends, except that values of the first were very high in some of the high elevation group soils.

The thickness of the A horizon showed a distinct trend from very thin (mean = 5 cm) at the top of the XY plane (the arid Jasper group), to thick (mean = 20 cm) at the bottom (the main Waterton group). It was, however, almost impossible to define or measure this horizon accurately in some of the very gravelly soils of the high elevation and main Waterton groups.

The stands in the arid Jasper and Red Deer River valley groups and a few of the main Waterton group had

high fecal pellet group counts due mainly to intensive grazing by elk. However, fecal group counts indicated that horses grazed the Red Deer River valley stands as intensively as elk.

When stand elevation was corrected for latitude by using a correction factor of 100 ft for every 15' of latitude (Hopkins, 1938), the stands showed a distinct trend from high elevation in the Red Deer River valley and high elevation groups and some of the stands in the central group to low elevation in the main Waterton group, with the arid Jasper group being intermediate.

Neither slope aspect nor slope angle showed any pattern.

Owing to variation in the type and degree of definition of the A horizon surface and the differential effect of moisture content, surface compaction data were very difficult to interpret. These results have therefore been discarded.

Insertion of the Twenty Intensive Study Site

Stands on the Ordination

It was of interest to place the intensive study site stands (studied in 1968) on the 51-stand ordination field to determine how accurately they represented their respective grassland types.

Indices of Similarity were calculated between each of the intensive area stands, (Nos. 52 to 57 at Henry House

flats, Jasper; Nos. 58 to 63 at the Hay Meadows, Waterton; Nos. 64 to 71 at the Badlands, Waterton), and the six end stands of the ordination, (X axis, Nos. 13 and 22; Y axis, Nos. 30 and 24; Z axis, Nos. 15 and 48). The position of each of these stands on the three axes was calculated by the method on p. 64 and thence the position of each stand in the XY, XZ and YZ planes found (Fig. 13; Appendix 7, p. 328).

The Henry House stands (Nos. 52 to 57) fit very well into the arid Jasper group, except No. 55 (the lodgepole pine forest stand) which stands above and to one side of the group.

The Badlands stands (Nos. 64 to 71) fit into the main Waterton group. Stand Nos. 64, 65, 67, 68, 69 and 70 are centrally located in this group and are representative of this grassland type, but Nos. 66 and 71 are on the edge, although closely related to this group. These last two stands were located in low-lying areas that were moister than the other stands and had a large number of species characteristic of more moist vegetation types.

The Hay Meadow stands (Nos. 58 to 63) represent a series from thin fescue prairie to moist sedge meadow and are therefore scattered across the ordination field. Stand Nos. 62 and 63 are in the main Waterton group. Numbers 58, 59, 60 and 61 form a linear series from No. 58 on the edge of the main Waterton group to No. 61 in the loosely-knit "centre group". Numbers 60 and 61 were geographically located adjacent to Nos. 9 and 10 and also appear thus on the ordination field.

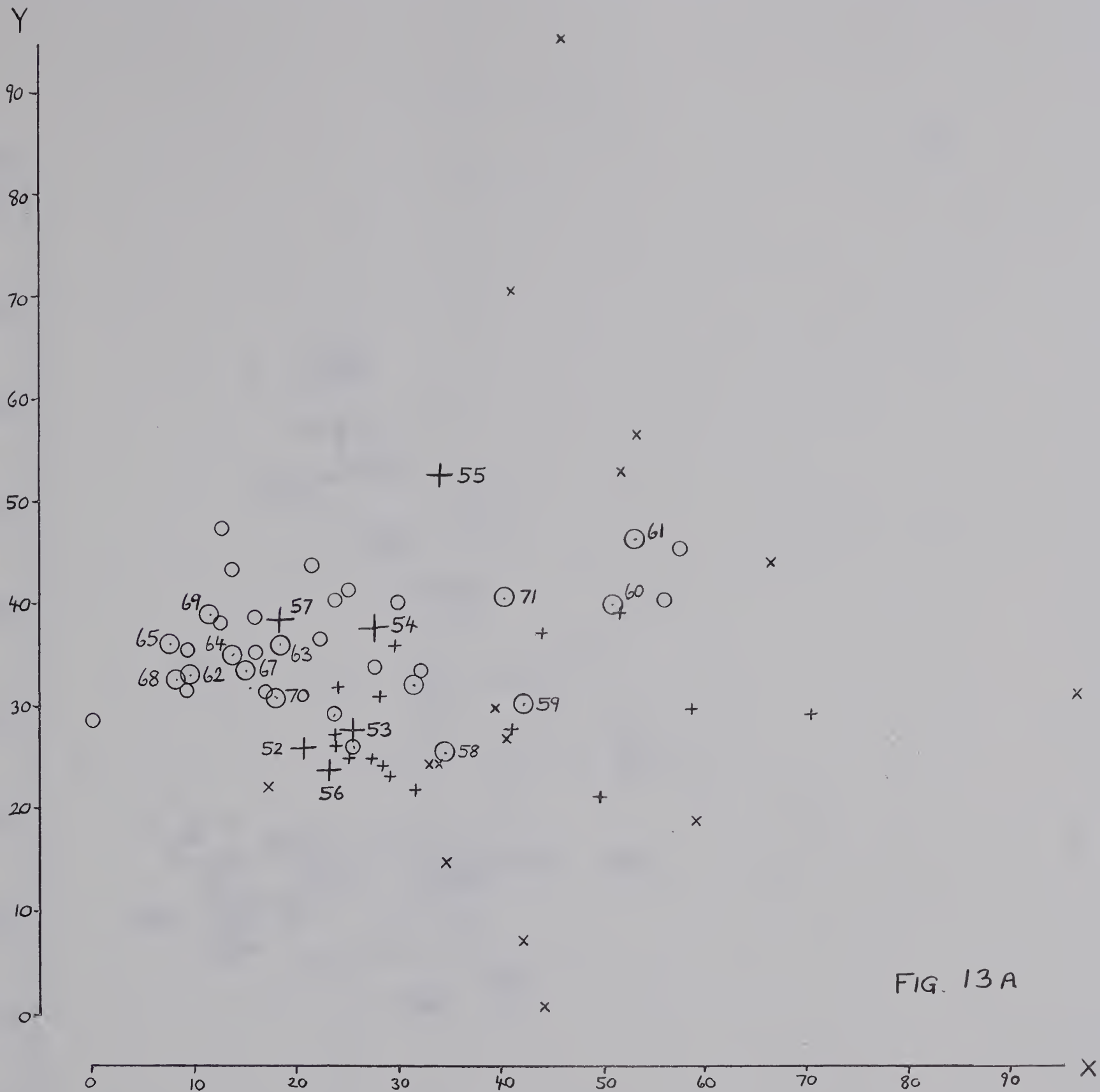


FIG. 13 A

The location of Intensive Study Site stands on the 51-stand ordination.

- A. on the XY plane.
- B. on the XZ plane.
- C. on the YZ plane.

Jasper stands (Nos. 52-57) shown as '+'

Waterton stands (Nos. 58-71) shown as 'o'

Stands sampled in 1967 (Nos. 1-51) shown as 'o' for Waterton, '+' for Jasper and 'x' for Banff, and not numbered: see Fig. 10, p. 66.

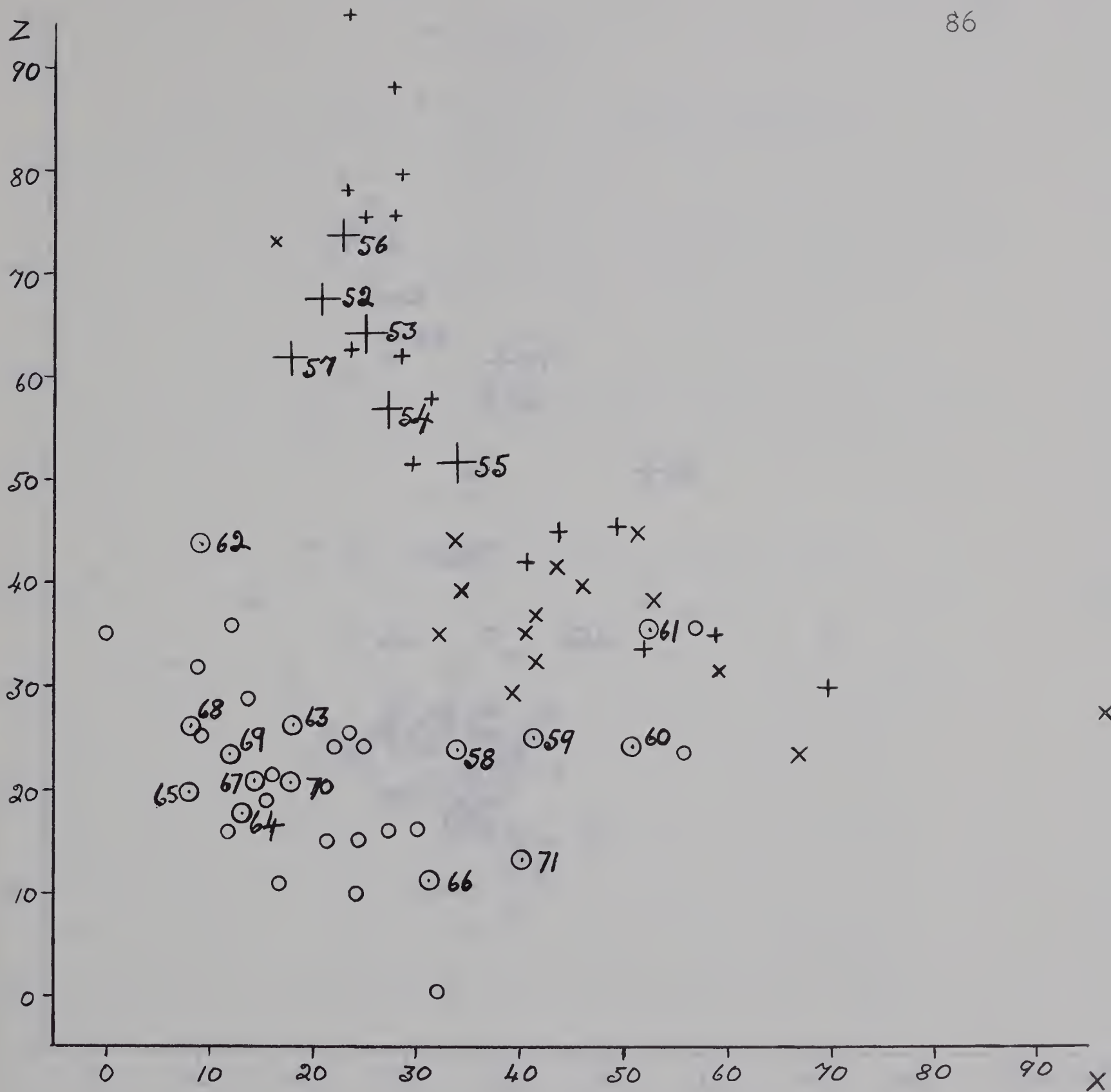
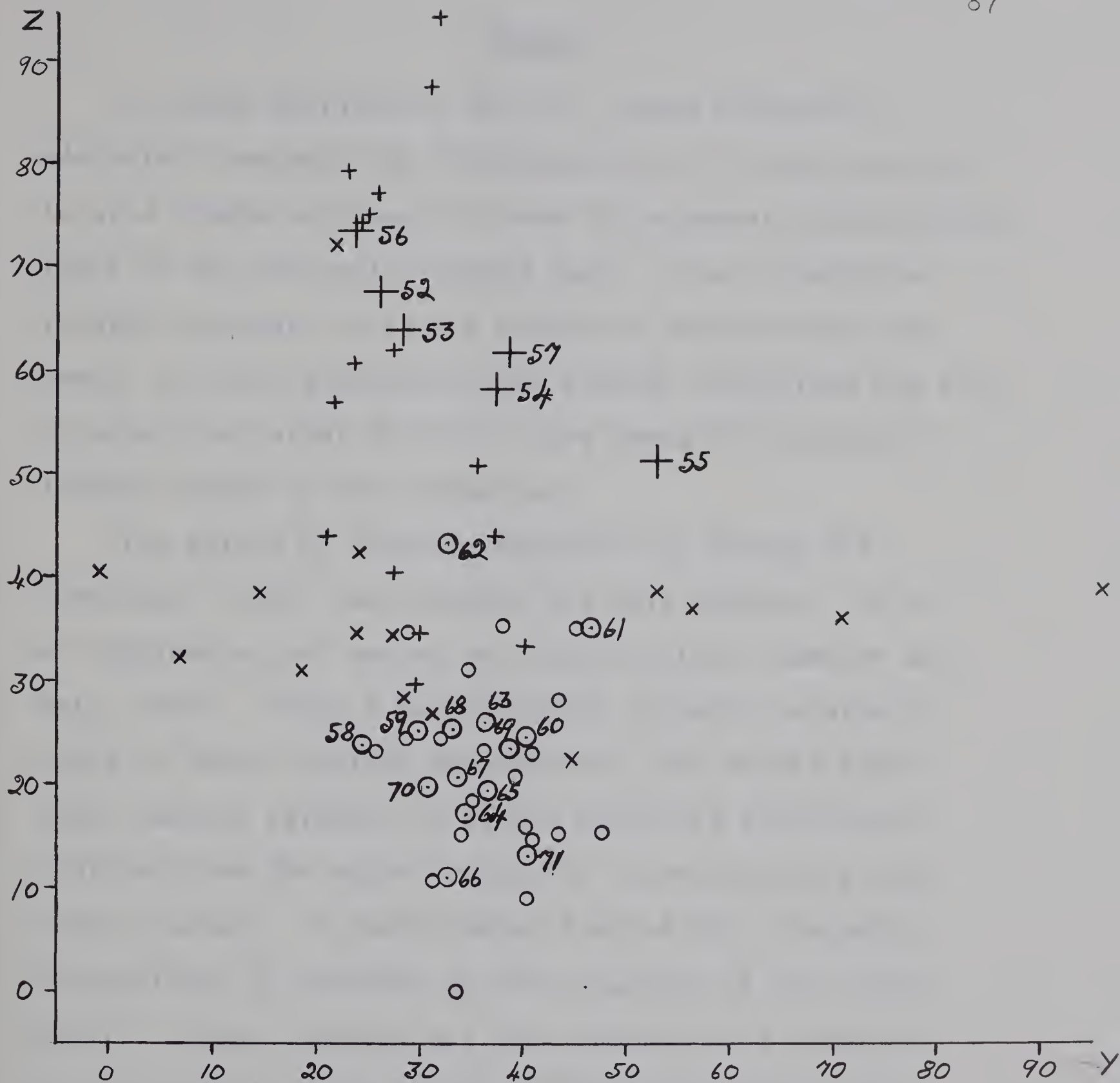


FIG. 13 B



CLUSTER ANALYSIS

Method

As noted previously, the 51 - stand ordination adequately portrays the relationships of the non-centrally located stands but does not seem to represent satisfactorily those of the centrally-located ones. It was therefore thought necessary to find a method to delimit more accurately the four grassland types already recognized and also to detect any other distinct types among the centrally-located stands on the ordination.

The method of "Cluster Analysis" of George and Carmichael (1966) was suitable for this purpose. It is an "agglomerative" method of classification (Lambert and Dale, 1967). Given a set of points (stands) located in space by their relative proximities, this method finds those subsets (groups) of points which are sufficiently isolated from the other subsets to be recognized as discrete clusters. A rank-ordered list of the interpoint similarities is searched to find clusters of very close points. These clusters are then added to and combined at successively lower levels of similarity until ultimately all the points are pooled in one large cluster.

The highest interpoint similarity is chosen to form the first cluster. All the remaining pairings are then searched in order of decreasing similarity to find

successively other points that are close enough to be considered part of that cluster. As each point is considered, it is judged for inclusion, using four criteria. Failure of the point to fulfil any one of the criteria results in its expulsion from the cluster.

The four criteria are as follows. The closest point to any member of a cluster may be included in that cluster unless:

1. Its average distance from the points in the cluster indicates a discontinuity in closeness ("Average Linkage" criterion).
2. Its distance from the closest point in the cluster indicates a discontinuity in closeness ("Best Link" criterion).
3. The point is near the centre of a non-spherical cluster which has enlarged in a direction other than towards the point before the point is considered for admission ("Ratios" criterion).
4. It is already a member of another cluster, in which case it is considered as a link between the two clusters.

The first three criteria are dependent upon two related resolution parameters which are lowered by a series of steps whose magnitude reflect successively lower levels of resolution.

On termination of a cluster, the similarities between the remaining points are searched for two stands

to form a second cluster. This method necessitates fixing a minimum level of interpoint similarity below which no clusters will form. Thus, the termination of cluster formation occurs when all the remaining stands have interpoint similarities which are below the required minimum value. If no interpoint similarities are above the required minimum, no clusters form at all.

Further details on this method, including the calculation of the two parameters and their relationships to the four criteria, are described in George and Carmichael (1966, p. 39-47).

Cluster Analysis of 71 Stands

Cluster analysis was applied to the 71 stands sampled in 1967 and 1968, using the Index of Dissimilarity (100 - Index of Similarity, p. 63) between pairs of stands to represent interpoint proximity. The computer program used to apply the cluster analysis technique to the data was based on that of Carmichael (1967).

The values "BEGIN" (the minimal level of interpoint similarity necessary to start a cluster) and "FINISH" (to set the lowest level of resolution) were set to the levels recommended by George and Carmichael (1966). Thus, "BEGIN" was set so that 90% of the interpoint similarities were below it and "FINISH" so that 95% of the interpoint similarities were above it; these values were approximately 0.50 and 0.065 respectively. Twelve equally-spaced levels

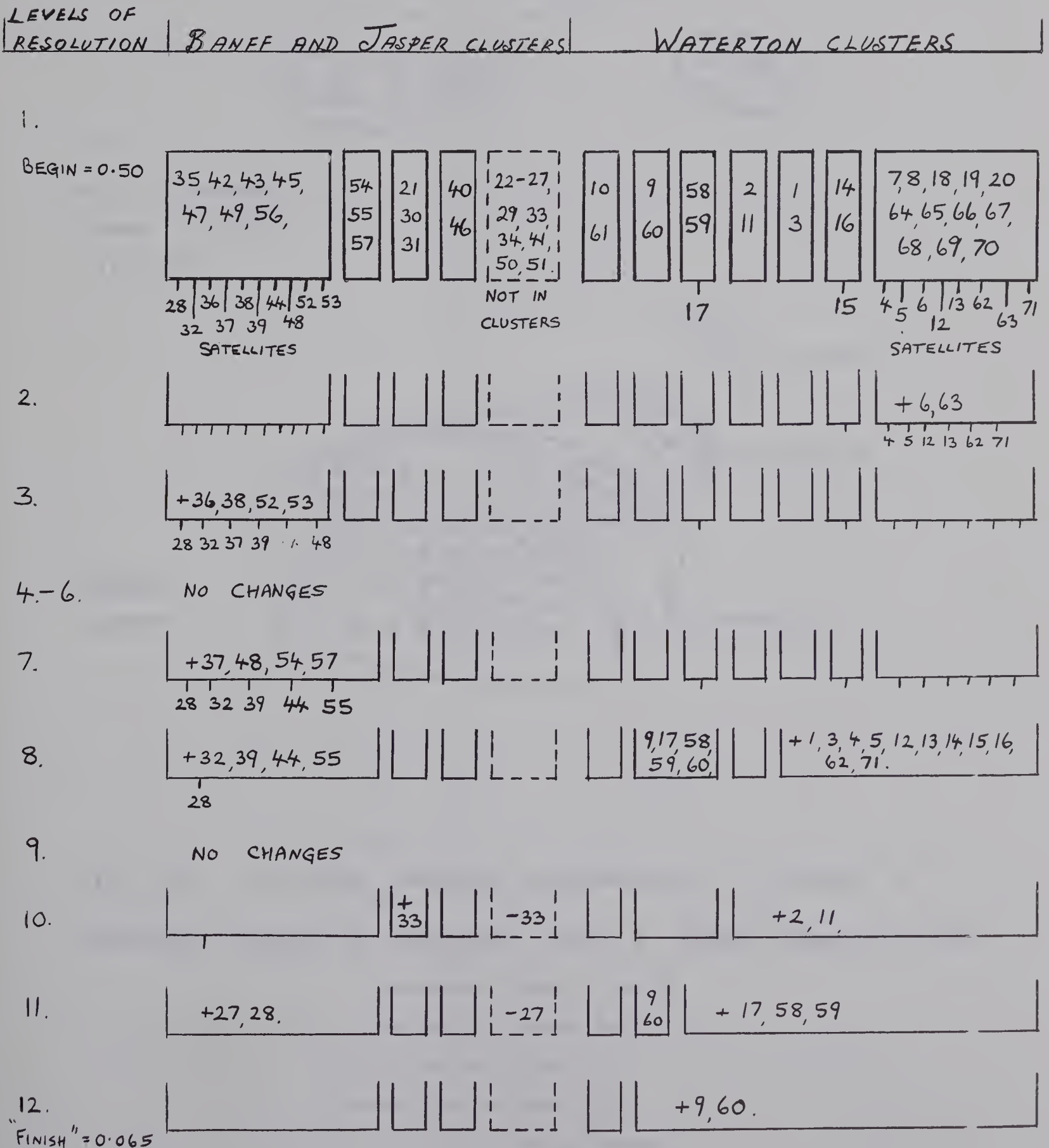
of resolution were specified.

Decisions on which levels of resolution gave the most meaningful clustering were essentially subjective. Decisions were made by comparison of clustering configurations at all twelve levels, with special reference to sudden changes in Average Linkage or other criteria derivatives upon the addition of stands to clusters. The most important criterion was thought to be the Average Linkage since this gave an indication of the relative "goodness" of the cluster. The other three criteria were essentially only to prevent the addition of stands when markedly non-spherical or unorthodox configurations were formed. In most cases, the most significant fact was an unusually large drop in the Average Linkage criterion, which indicates that the cluster so terminated was relatively tight.

On studying the development of clusters with decreasing resolution, the complete lack of connection between the Waterton stands and the Banff-Jasper stands became apparent (Figs. 14 and 15). In effect, the two groups of stands (34 in Waterton; 37 in Banff and Jasper) could be considered separately, as no linkages were developed between them at any level of resolution.

After 12 levels of resolution, all but two of the 34 Waterton stands were absorbed into one large Waterton cluster. However, after 12 levels of resolution, 10 of the 37 Banff-Jasper stands were left as unrelated,

FIG. 14 CLUSTER ANALYSIS OF 71 STANDS AT 12 LEVELS OF RESOLUTION, USING A "BEGIN" VALUE OF 0.50



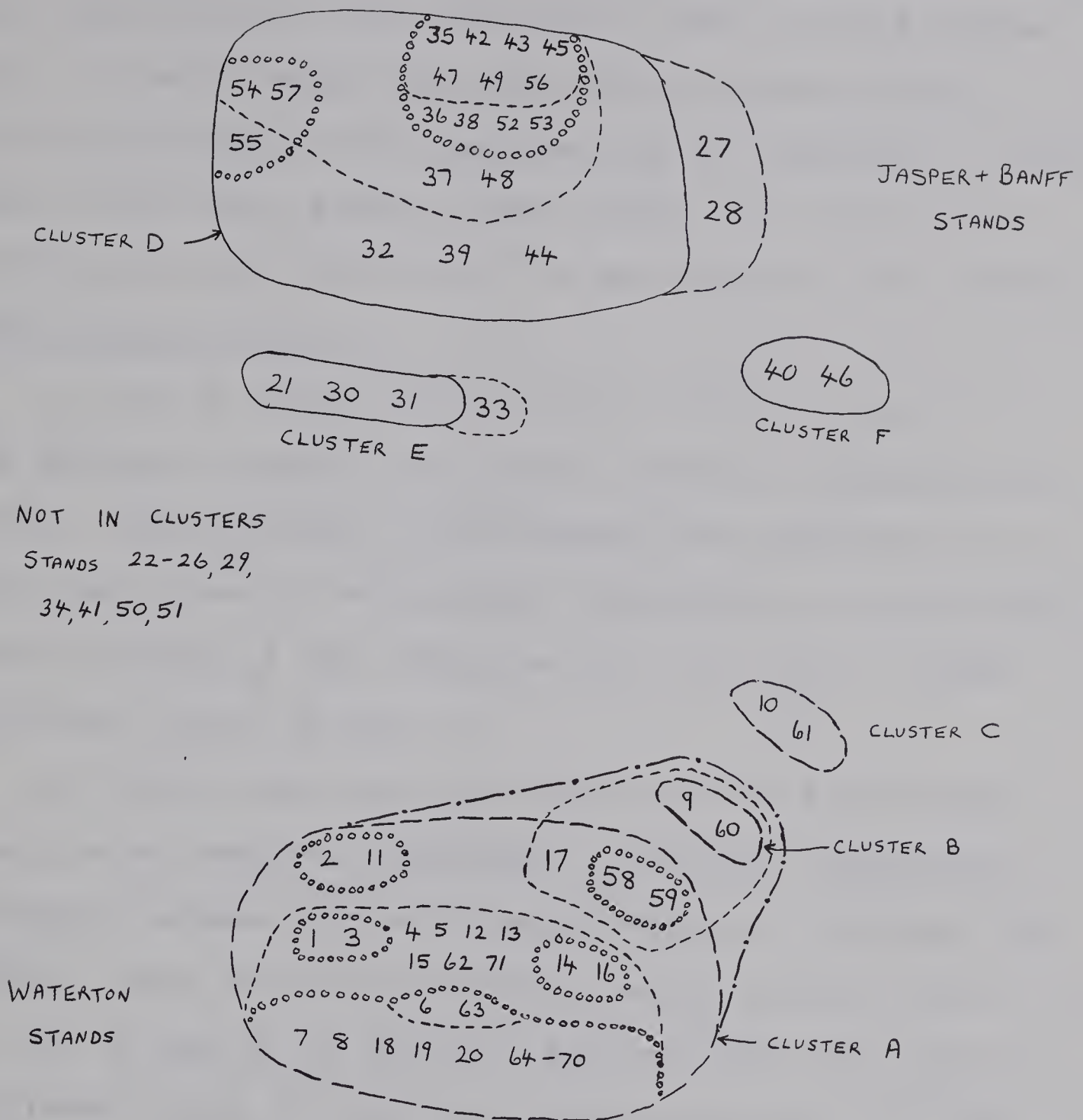


FIG. 15 CLUSTER ANALYSIS CONFIGURATION OF 71 STANDS AT MEANINGFUL LEVELS OF RESOLUTION, USING A "BEGIN" VALUE OF 0.50

single-stand clusters. These 10 stands included Nos. 23-26, the high-elevation group detected by the 51-stand ordination. It was thought that the failure of the cluster analysis to detect this group was due to the value of "BEGIN" used; within this group of four stands, all inter-stand similarities were less than 0.50 and therefore the cluster never began to form.

To try to detect loose clusters of this type, it was decided to repeat the cluster analysis, changing the "BEGIN" value to 0.25. This started the clustering at a much lower level of resolution, resulted in a considerable simplification of the configurations and left no stands unrelated (Figs. 16 and 17).

As before, the Waterton stands and the Banff-Jasper stands were completely separate. There was considerable agreement between the two cluster analyses. Changing the "BEGIN" value to 0.25 detected two extra clusters (Nos. 22, 23, 25, 35 and 50; 24 and 26), both of which were left as unrelated stands in the first cluster analysis. At the same time, a great deal of sensitivity was lost, since both large clusters were made larger, and therefore less tight at level 1. A more detailed discussion of the resolution of clusters may be found in Appendix 10, p. 339.

To summarise these cluster analyses, the 71 stands may be grouped most meaningfully as follows:

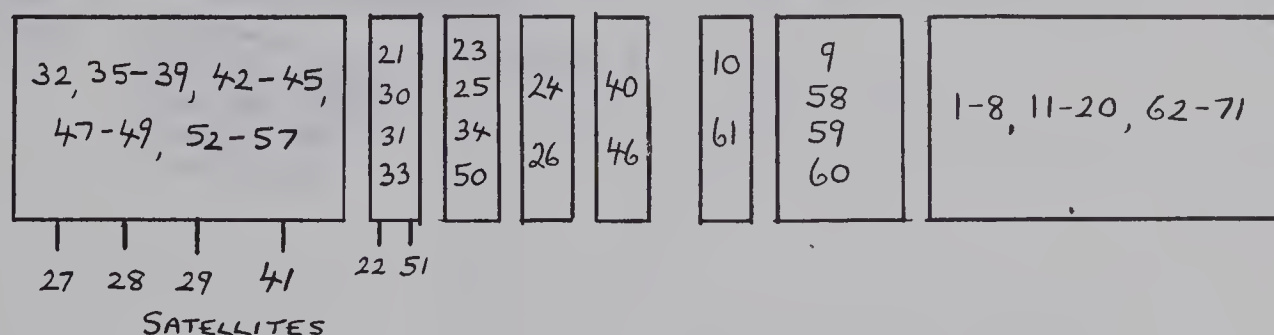
Cluster A. A main Waterton cluster of 30 stands (Nos. 1-8, 11-20, 58, 59, 62-71) which includes a closely-

FIG. 16 CLUSTER ANALYSIS OF 71 STANDS AT 12 LEVELS OF RESOLUTION, USING A "BEGIN" VALUE OF 0.25

LEVELS OF RESOLUTION	BANFF AND JASPER CLUSTERS	WATERTON CLUSTERS
----------------------	---------------------------	-------------------

1.

BEGIN = 0.25



2.

NO CHANGES

3.



4, -7.

NO CHANGES

8.



9.



10.



11-12.

NO CHANGES

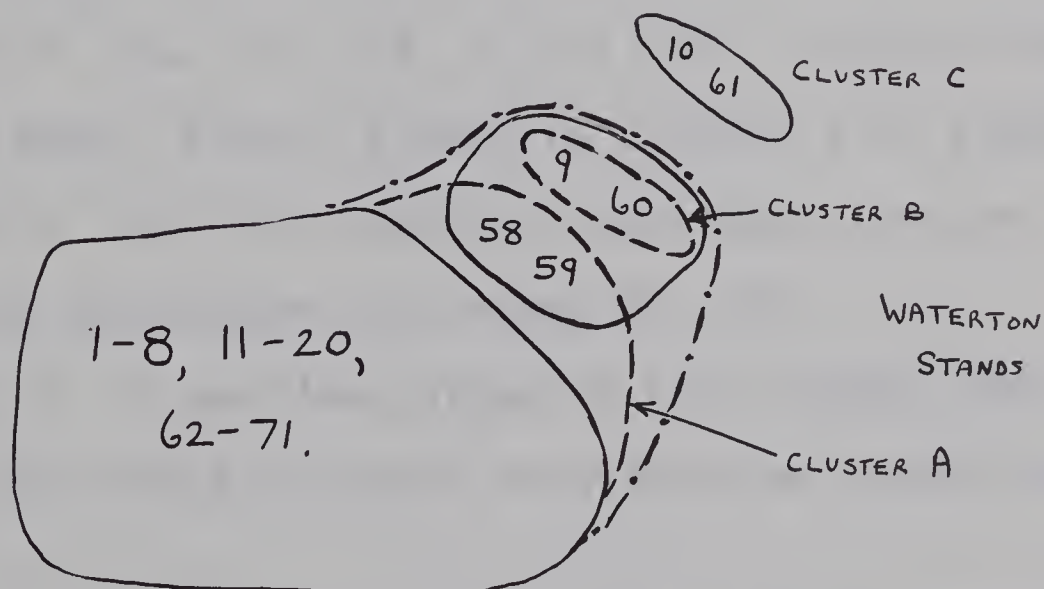
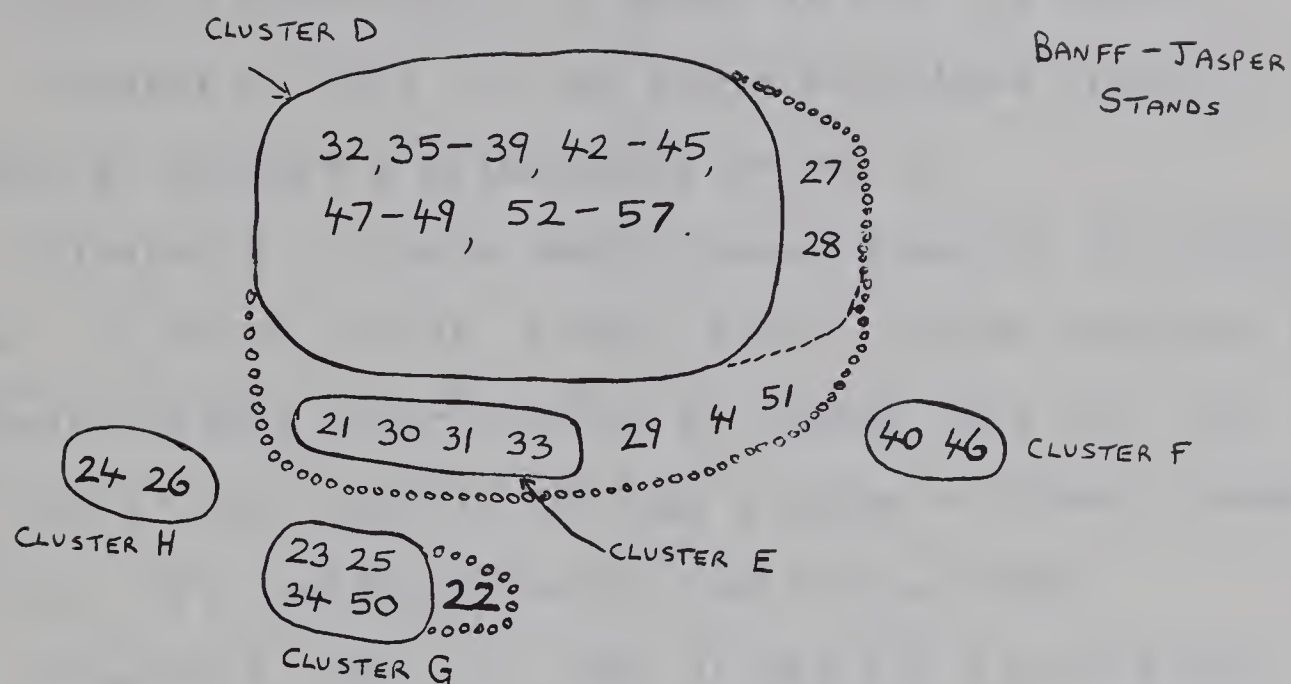


FIG. 17 CLUSTER ANALYSIS CONFIGURATION OF 71 STANDS AT MEANINGFUL LEVELS OF RESOLUTION, USING A "BEGIN" VALUE OF 0.25

—————	LEVEL 1
- - - - -	LEVEL 3
— • — • — • —	LEVEL 9
oooooooooooooooo	LEVEL 10
- - - - -	OTHER LEVELS

related inner core of 14 stands (Nos. 6-8, 18-20, 63-70).

Cluster B. Nos. 9 and 60; a two-stand cluster linked to cluster A principally by means of Nos. 58 and 59.

Cluster C. Nos. 10 and 61; a two-stand cluster linked to cluster B principally by No. 9.

Cluster D. A main Banff-Jasper group of 19 stands (Nos. 32, 35-39, 42-45, 47-49, 52-57), which includes a closely-related inner core of 11 stands (Nos. 35, 36, 38, 42, 43, 45, 47, 49, 52, 53, 56) and a group of three stands (Nos. 54, 55, 57), distinguished by their tree cover.

Cluster E. Nos. 21, 30, 31 and 33; a four-stand cluster linked to cluster D by stand No. 32.

Cluster F. Nos. 40 and 46; a two-stand cluster linked to cluster D by stand No. 41.

Cluster G. Nos. 22, 23, 25, 34, 50; a rather loose cluster of stands, poorly linked to cluster D by stand No. 33.

Cluster H. Nos. 24 and 26; a two-stand cluster, poorly linked to cluster D by stand No. 55.

Cluster I. A residual group of five stands (Nos. 27, 28, 29, 41, 51) which are best considered as satellites of cluster D.

The validity of clusters B, C, F and H as distinct grassland types is doubtful because of their small representation. They will, however, be described as units and treated as examples of vegetation types which occupy relatively small areas and have therefore not been adequately sampled in this study.

Integration of the Results of Cluster Analysis and Ordination

A first comparison of the stand groupings achieved by these two classification methods was done by outlining clusters on the ordination field (Fig. 18). It can be seen that clusters A, D and E correspond closely to the groups named respectively the main Waterton group, the arid Jasper group and the Red Deer River valley group on the ordination field. The fourth clear ordination grouping, the Banff high-elevation group has not been substantiated, having been split into two and represented in clusters G and H. Clusters B, C and F are two-stand clusters which were undetected by the ordination technique. Cluster analysis has delimited the groupings already detected by the ordination and, more important, has sorted out the relationships of the stands located centrally on the ordination field.

Species Composition of Stand Clusters

An effective way of determining which species contribute most to the definition of clusters and hence to the major grassland types is to rearrange and classify them in the manner followed by the phytosociologists of the Zürich-Montpellier school (Braun-Blanquet, 1964) in the construction of an association table.

The stand clusters were arranged in a linear sequence intended to represent as closely as possible the vegetational

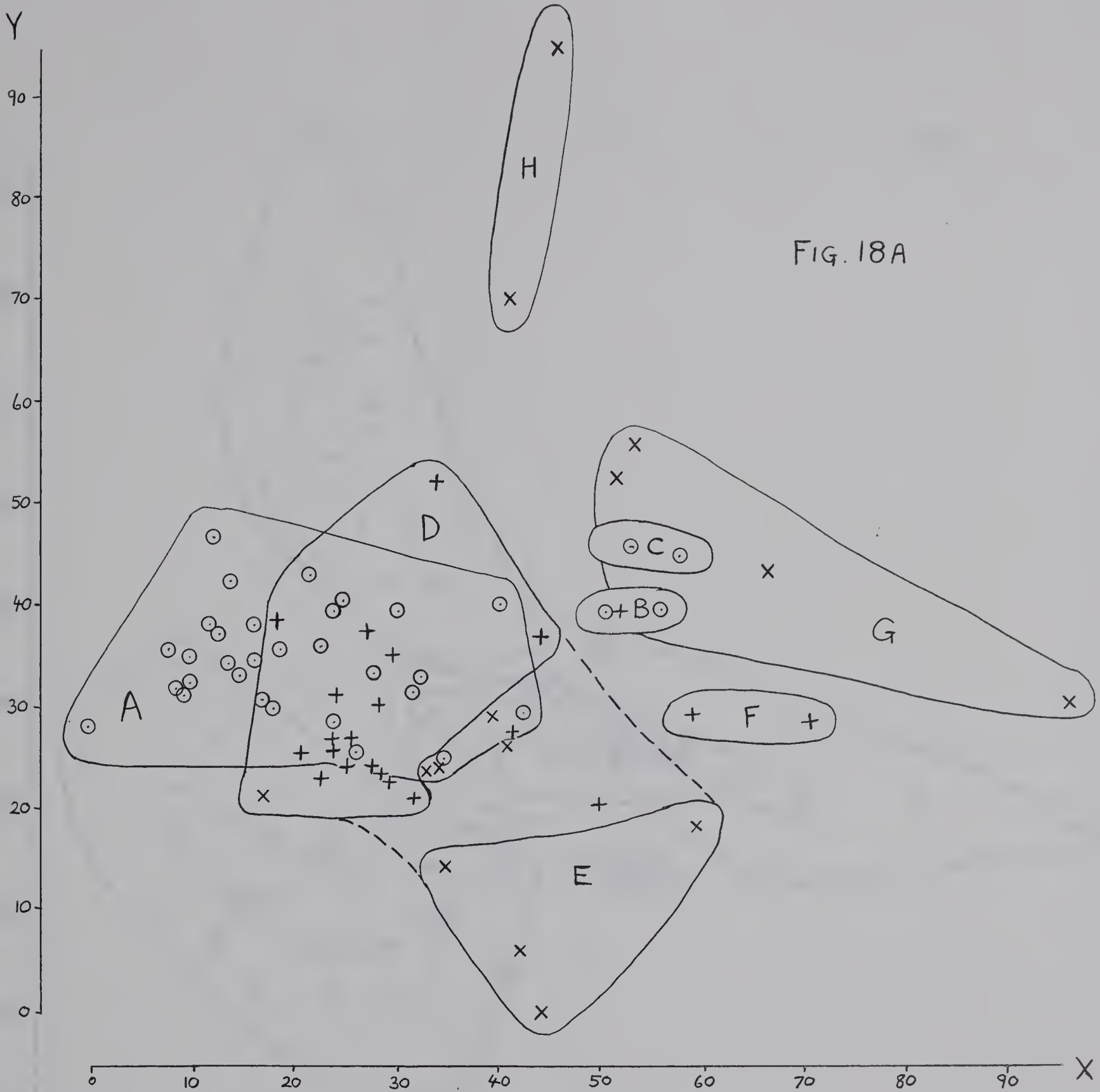


FIGURE 18

The configuration of clusters on the 71-stand ordination

- A. on the XY plane.
- B. on the XZ plane.
- C. on the YZ plane.

Clusters A-H enclosed with solid lines; outer satellite stands of Cluster D enclosed with a broken line.

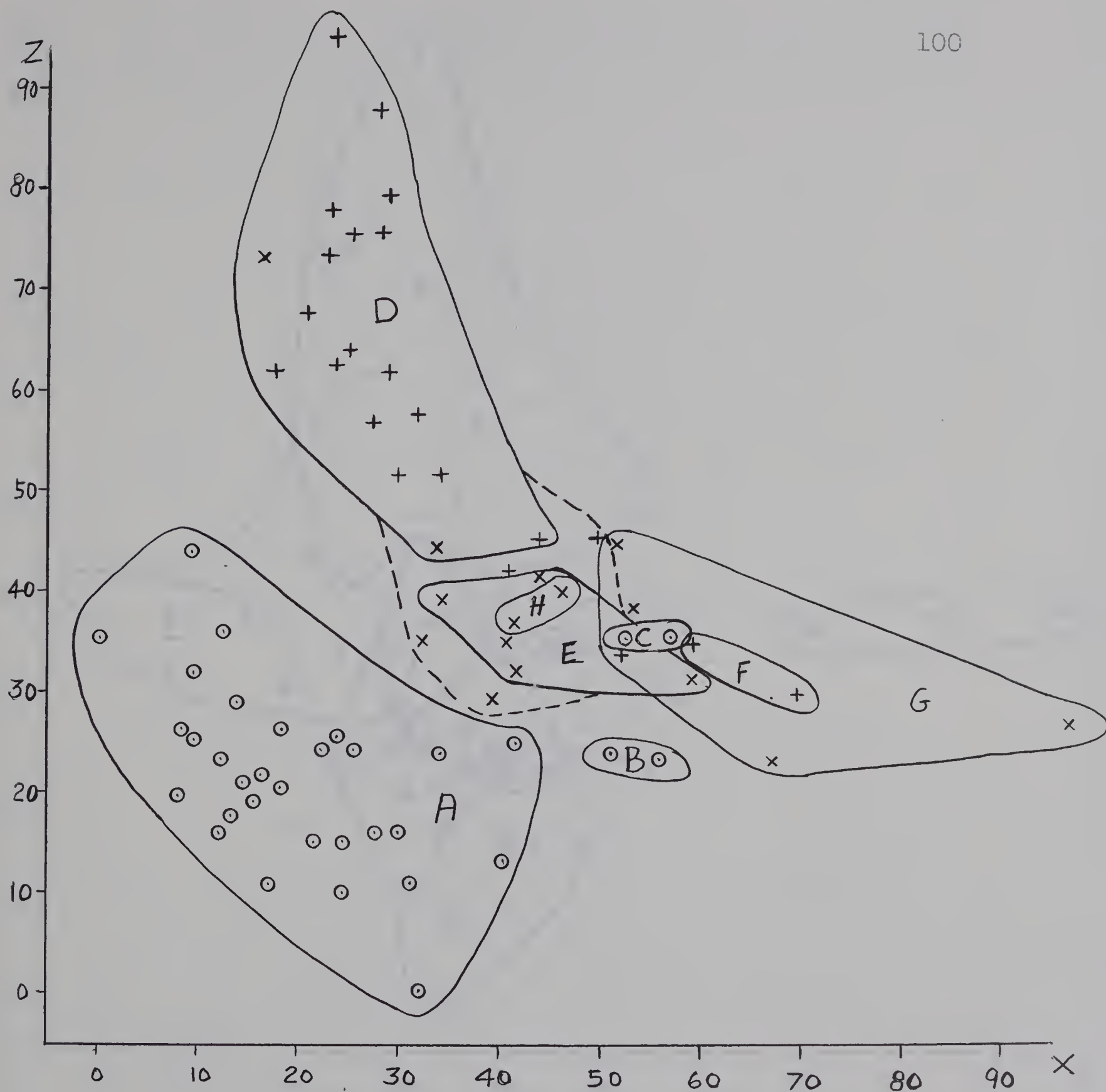


FIG. 18 B

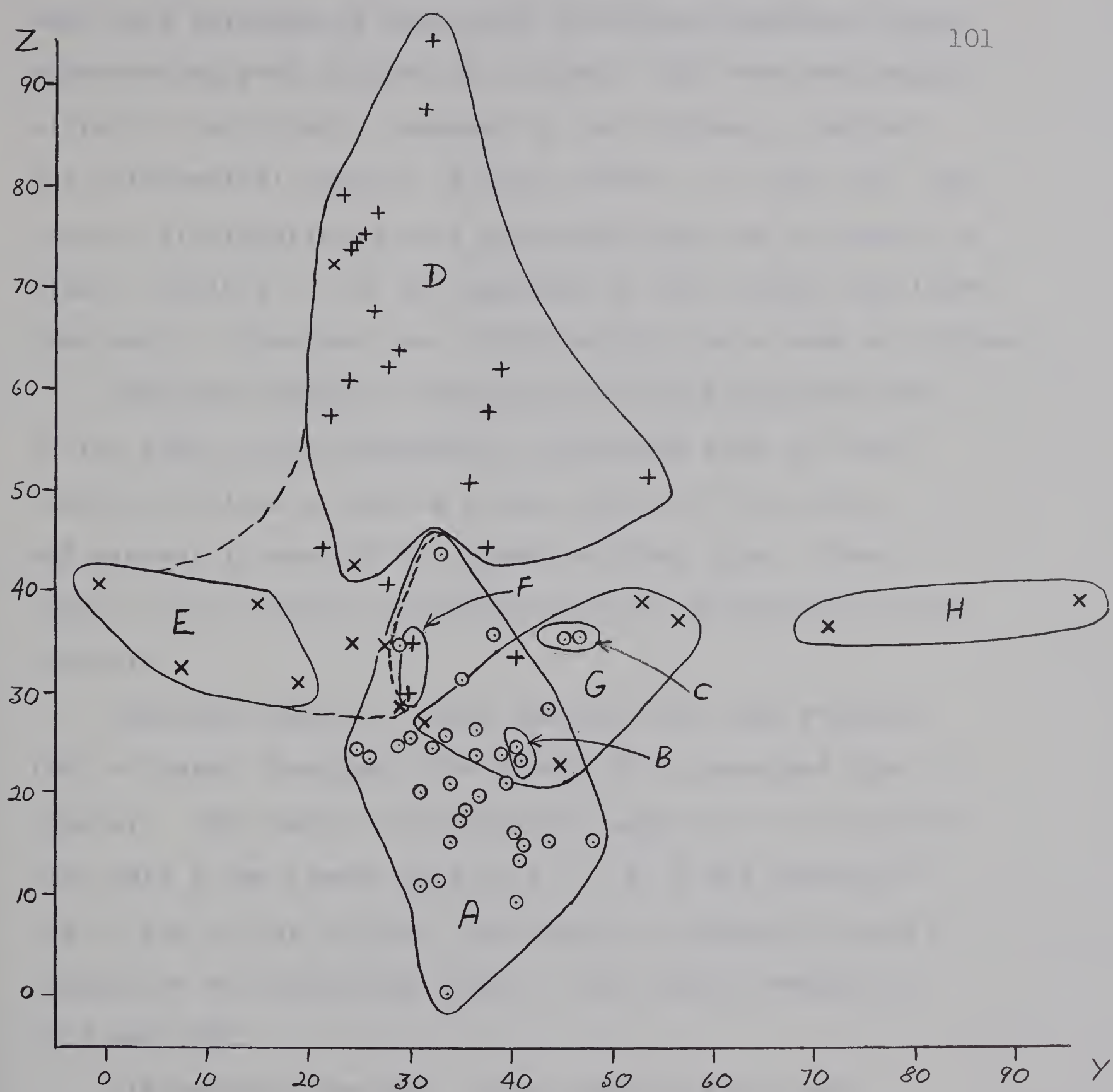


FIG. 18 C

and geographical relationships of the clusters. The species were then arranged in rows, with the Cover-abundance value representing each species in a stand. The rows were manipulated to form blocks composed of the Dominant, Constant and Differential species of each cluster. In this way, the species distinguishing each grassland type can be seen at a glance (Table 4). For the purposes of this study, the terms "Dominant", "Constant" and "Differential" were used as follows:

Dominant species: those species which provided most of the plant cover throughout a grassland type or stand cluster, defined as having a mean cover of 3% or more and present in most of the stands of that type. These species were chiefly responsible for the definition of the clusters.

Constant species: those species with high Presence (80% or more) throughout the stands of a grassland type or cluster. This term is not strictly applicable to clusters with only a few stands such as B, C, F, H and possibly E and G, and is not strictly applicable to clusters A and D because of the differing sizes of the stands sampled in 1967 and 1968.

Differential species: those species which were either more Abundant (Cover-abundance) or more Constant, or both, in one grassland type or stand cluster than in one or more others of those studied.

To include all 291⁶ vascular species plus bryophytes

⁶ To the 281 species recorded in 1967, 10 were added from the intensive site study.

TABLE 4. ASSOCIATION TABLE.

[illegible]

TABLE 4. Cont'd.

[illegible]

and lichens would have resulted in a very long table, in which the large number of uncommon species would complicate the definition of meaningful species blocks. Therefore, the following criteria were used to eliminate species and so make the table manageable.

1. All species, including terrestrial bryophytes and lichens, were included which had mean covers of 0.5% or more, as well as a Presence of 50% or more in any of the clusters or cluster cores represented by more than three stands, *e.g.*, A, D, E and G.

2. Species were included which had a mean cover of 3.0% or more in the two- or three-stand clusters such as F, H, B and C.

3. Also included were those species with a Presence of 80% or more in any of the larger clusters, regardless of mean cover.

Some subjectivity was necessary in arranging the table to show species blocks, since certain species did not quite fit the criteria but were, however, considered important Differential species, *e.g.*, *Geranium viscosissimum* and *Lithospermum ruderae* in Cluster A.

Cluster A. This group of 30 stands is characterized by the Dominance of the grasses *Festuca scabrella*, *F. idahoensis* and *Danthonia parryi*, the forbs *Lupinus sericeus* and *Galium boreale*, and the club moss *Selaginella densa*. The following species were Constants: the grasses *Koeleria cristata*, *Helictotrichon hookeri* and *Stipa columbiana*,

and the forbs *Achillea millefolium*, *Anemone multifida*, *Anemone patens* var. *wolfgangiana*, *Aster laevis* var. *geyeri*, *Cerastium arvense*, *Gaillardia aristata*, *Penstemon confertus* and *Potentilla gracilis*, as well as all the Dominants except *Danthonia parryi*, this species having a constancy of only 77%. The most important species constituting the inner core of 14 stands were these Constants and Dominants, together with the grass *Agropyron spicatum* and the forbs *Antennaria umbrinella* and *Erigeron caespitosus*, the shrub *Rosa woodsii* and the moss *Tortula ruralis*. Other species which were prominent in Cluster A without, however, attaining an overall position of Dominance or Constancy were the grasses *Agropyron dasystachyum*, *A. trachycaulum* var. *unilaterale* and *Danthonia intermedia*, and the forbs *Agoseris glauca*, *Geranium viscosissimum*, *Lithospermum ruderales* and *Monarda fistulosa* var. *menthaefolia*.

There were clearly a large number of species Differential to this cluster, the most prominent being *Agropyron spicatum*, *Festuca idahoensis*, *Stipa columbiana*, *Antennaria umbrinella*, *Geranium viscosissimum*, *Lithospermum ruderales* and *Lupinus sericeus*.

A number of species were far more prominent and were often the Dominants in the five stands which formed the outermost satellites of Cluster A (Nos. 2, 11, 17, 58, 59). These species were the grasses *Bromus pumpellianus* and *Poa pratensis* and the forbs *Lithospermum ruderales*, *Smilacina stellata* and *Taraxacum officinale*. These stands were the

most mesic in the cluster, all being in low-lying meadows adjacent to lakes or rivers. In habitat and vegetation, they appeared to be intermediate between Cluster B and the bulk of Cluster A.

The stands of cluster A may conveniently be termed "*Festuca-Danthonia* Prairie", and the five more mesic stands which are considered as a variant of this type can be termed "*Poa pratensis-Smilacina* Meadows".

Cluster B. This cluster consisted of only two adjacent stands which were examples of the many small, low-lying, grass meadows close to the Waterton and Belly rivers in Waterton Lakes National Park.

The Dominant species were the grasses *Bromus inermis*, *Phleum pratense* and *Poa pratensis*, and the forbs *Agoseris glauca*, *Aster laevis* var. *geyeri*, *Fragaria virginiana* var. *glauca*, *Galium boreale*, *Monarda fistulosa* var. *menthaefolia*, *Taraxacum officinale* and *Thalictrum venulosum*. The grasses *Agropyron dasystachyum* and *Stipa columbiana*, the sedge *Carex praegracilis* and the forbs *Achillea millefolium*, *Geum triflorum*, *Smilacina stellata* and *Vicia americana* were also prominent.

Cluster C. This cluster consisted of only two adjacent stands in the same area as Cluster B. They were examples of low-lying sedge meadows common in the Waterton and Belly River valleys.

Here the Dominant species were *Festuca elatior* and *Phleum pratense*; *Carex praegracilis* and *Juncus balticus*;

Fragaria virginiana var. *glauca*, *Pedicularis groenlandica*, *Ranunculus acris*, *Taraxacum officinale* and *Trifolium repens*. The grass *Poa pratensis*, the forb *Thalictrum venulosum* and a number of *Carex* spp. were also prominent in these sedge meadows.

It seems probable that several of the sedge meadow species are introduced, e.g., *Festuca elatior*, *Bromus inermis*, *Phleum pratense*, *Trifolium repens* and *T. pratense*, which are known introduced fodder species (Moss, 1959). It is therefore suggested that stands 9, 10, 60 and 61 in their present state should not be regarded as native vegetation types but rather as resulting from the activities of man.

Cluster D. Most of the stands in this group were arid and often heavily-grazed grasslands, many of those in the inner core being in the Athabasca River valley in Jasper. They had relatively low species diversity.

The Dominants in this grassland type were the grasses *Calamagrostis montanensis* and *Koeleria cristata*, and the forbs *Antennaria nitida/rosea*,⁷ *Artemisia frigida* and *Astragalus striatus*. *Calamagrostis* and *Artemisia* were especially prominent in the inner core of 11 stands. These Dominants together with the following Constants formed a very sparse but distinctive vegetation. *Agropyron*

⁷ See footnote, p. 59

dasystachyum, *Bromus pumpellianus*, *Erigeron caespitosus*, *Linum lewisii*, *Senecio cymbalarioides* and *Solidago decumbens*.

A number of other species were prominent in this grassland type: the grass *Poa interior*; the sedge *Carex eleocharis*; the forbs *Anemone multifida*, *A. patens* var. *wolfgangiana*, *Androsace septentrionalis*, *Gaillardia aristata*, *Galium boreale*, *Oxytropis sericea* var. *spicata*, and the lichen *Peltigera canina*.

Three species (*Elymus innovatus*, *Arctostaphylos uva-ursi*, *Juniperus communis*) were especially prominent in and Differential to three stands forming a subordinate cluster inside Cluster D. These stands were pine forest (No. 55) and pine savanna (Nos. 54 and 57) and were situated in the same locality as the arid grassland stands of the Athabasca River valley, especially Nos. 43, 45, 49, 52, 53 and 56. In the grasslands they represented an element which is usually forest understory and did not occur in areas away from trees.

The stands in Cluster D are named "*Koeleria-Calamagrostis montanensis* Grassland" after their two Dominant grasses.

Cluster E. These four Banff stands from the Red Deer River valley (Nos. 21, 30, 31) and Bow River valley (No. 33) were closely related to Cluster D and were absorbed by it at a low level of resolution.

The Dominants were *Helictotrichon hookeri*, *Koeleria cristata* and *Poa pratensis*; and *Antennaria nitida/rosea*⁸

⁸ See footnote, p. 59

and *Geum triflorum*. The following species were also prominent: *Agropyron trachycaulum* var. *unilaterale*, *Bromus pumpellianus*; *Carex eleocharis*; *Androsace chamaejasme*, *Cerastium arvense*, *Potentilla pensylvanica*; *Selaginella densa*; and *Peltigera canina*.

Besides many species representative of *Koeleria-Calamagrostis montanensis* Grasslands, e.g., *Agropyron dasystachyum*, *Koeleria cristata*, *Antennaria nitida/rosea*, *Artemisia frigida* and *Peltigera canina*, Cluster E stands had species more typical of the *Festuca-Danthonia* Prairie, e.g., *Festuca scabrella*, *Helictotrichon hookeri*, *Cerastium arvense*, *Potentilla gracilis*, *Tortula ruralis* and *Selaginella densa*.

Cluster E stands are named "*Koeleria-Geum triflorum* Grassland".

Cluster F. These two stands (Nos. 40, 46) were in the flat bottoms of small valleys in the Buffalo Prairie area of Jasper National Park. They were isolated from most of the other Jasper grasslands and had a distinctive species composition.

The Dominants were *Poa pratensis*, *P. palustris*, *Hordeum jubatum*, *Agropyron trachycaulum* var. *unilaterale*; *Carex eleocharis*; and *Potentilla anserina* and *P. pensylvanica*. *Hordeum* and *Potentilla anserina* were found only in the Cluster F stands. Species prominent in the other grassland types were not prominent in these stands.

The distinctiveness of Cluster F grasslands is probably

due to the overwhelming Dominance of a few species, two of which may have been introduced by man's activities (*Poa pratensis* and *Hordeum jubatum*).

These stands, although perhaps not representing a distinct grassland type, are named "*Poa-Hordeum jubatum* Grassland".

Cluster G. These five stands (Nos. 22, 23, 25, 34, 50) were all mesic, level meadows at higher elevations than most of the other stands. They were in the subalpine or montane zone, were small and isolated from each other and surrounded by the predominant spruce-fir-pine forest of these zones.

Their species composition was distinct from any of the other grassland types; the Dominants were *Danthonia intermedia*, *Stipa richardsonii*, *Poa pratensis*; *Potentilla fruticosa*, *Salix glauca*, *Arctostaphylos uva-ursi*; *Fragaria virginiana* and *Penstemon confertus*.

Other prominent species were *Bromus pumpellianus*, *Agropyron trachycaulum* var. *unilaterale*, *A. dasystachyum* and *Elymus innovatus*; *Betula glandulosa*; and *Potentilla gracilis*. Shrubs were more prominent here than in any of the other grassland types, except that in cluster H.

Species more often found in xerophytic coniferous forest understory were present, e.g., *Fragaria*, *Arctostaphylos* and *Elymus*.

This grassland type is termed "*Stipa richardsonii* Subalpine Grassland".

Cluster H. These two stands (Nos. 24, 26) were also at relatively high elevations (5,500 ft), on steep S-facing slopes with no forest cover, possibly because of snow slides. Their soils, of very coarse, angular gravel and boulders, with very little profile development, suggested rock slides.

The Dominants, all common coniferous forest understory species, were *Elymus innovatus*; *Amelanchier alnifolia*, *Arctostaphylos uva-ursi*, *Rosa acicularis*, *Rubus strigosus*; and *Fragaria virginiana*, *Galium boreale* and *Hedysarum sulphurescens*.

Agropyron dasystachyum, *Bromus pumpellianus*, *Poa pratensis*, *Juniperus communis* and *Vicia americana* were prominent in one of the stands.

This vegetation type has a prominent shrub stratum and so is termed "*Elymus innovatus* Subalpine Shrub Savanna".

GRASSLAND TYPES AND ENVIRONMENT

Festuca-Danthonia Prairie

1. Vegetation

The Dominant, Constant and Differential species of this grassland type are listed on pages 105-7 and in Table 4, pages 103-4. This grassland is characterized by a great species diversity compared with the other grassland types in this study. There was an average of 58 vascular species per 200 ft x 300 ft (= 61 x 91 m) stand for *Festuca-Danthonia* Prairie but only 37 for the other grassland types combined.

However, many of these 58 species contributed very little to the total vegetation cover and only the following had mean cover values of 3% or more: *Festuca scabrella* (14.2), *F. idahoensis* (11.6) and *Danthonia parryi* (7.9); *Lupinus sericeus* (6.5) and *Galium boreale* (4.2); *Selaginella densa* (6.9). The mean total cover of vascular plant species was approximately 102%.

The large, dark green, narrow-leaved bunches of *Festuca scabrella* and the large, bright green, broad-leaved bunches of *Danthonia parryi* were far more conspicuous than the small, blue-green, needle-leaved bunches of *Festuca idahoensis* (Plate 1). These three bunch grasses, the conspicuous clumps of *Lupinus sericeus* and the somewhat less conspicuous *Galium boreale* characterize this grassland type.



(a)



(b)

Plate 1.

- (a) *Festuca-Danthonia* Prairie; stand 6, Waterton Lakes National Park; has been very lightly grazed by horses (June, 1967).
- (b) Detailed view of *Festuca-Danthonia* Prairie; stand 15, Waterton Lakes National Park; shows bunch habit of *Festuca scabrella* and *F. idahoensis* (July, 1967).

All the prominent grasses were of the bunch type. The only rhizomatous grasses of note were *Poa pratensis* and *Bromus pumpellianus*, which occurred in abundance only in the more mesic stands.

The following tall forbs, although low in total cover, were conspicuous when in flower: *Aster laevis* var. *geyeri*, *Gaillardia aristata*, *Geranium viscosissimum*, *Hedysarum sulphurescens*, *Lithospermum ruderales*, *Monarda fistulosa* var. *menthaefolia* and *Potentilla gracilis*.

Selaginella densa and a number of other common, low-growing species such as *Danthonia intermedia*, *Koeleria cristata*, *Achillea millefolium*, *Antennaria umbrinella*, *Cerastium arvense* and the moss *Tortula ruralis* were far less conspicuous. They tended to fill in the gaps between the larger bunch grasses and forbs, thus forming an understory.

The structure of this grassland is of three strata: a tall forb-bunch grass stratum, up to 70 cm high, the forbs being those mentioned above and the Dominants being *Festuca scabrella*, *Danthonia parryi* and *Lupinus sericeus*; a <25 cm high understory of *Festuca idahoensis*, *Koeleria cristata*, *Danthonia intermedia*, *Stipa columbiana*, *Carex* spp., *Achillea millefolium* and *Galium boreale*; and, in the drier and more exposed areas, a mat-like ground cover (<5 cm high) of *Selaginella densa*, *Tortula ruralis*, *Antennaria umbrinella*, *Arenaria* spp., *Cerastium arvense* and *Phlox hoodii*.

This distinct stratification seems to be related to

the sequence of flowering, as many of the plants in the lower strata begin flowering earlier than those in the upper stratum.

The first common species to flower in 1967 and 1968 was *Anemone patens* var. *wolfgangiana* which was already fruiting in the second week in June. By mid-June, several small annuals and low-growing, perennial forbs were flowering. These included *Antennaria umbrinella*, *Arabis* spp., *Arenaria rubella*, *Cerastium arvense*, *Draba nemorosa*, *Erysimum inconspicuum*, *Oxytropis sericea* var. *spicata*, *Sisyrinchium montanum* and *Taraxacum officinale*. Most of the forbs and grasses began flowering in late June or in July. A small group of species did not begin flowering until the last week in July or later; the commonest of these were *Erigeron caespitosus*, *Chrysopsis villosa*, *Gaillardia aristata*, *Solidago missouriensis* and *Monarda fistulosa* var. *menthaefolia*. The last species to flower was *Aster laevis* var. *geyeri*. All of this group were in the family Compositae except *Monarda* (Labiatae).

There was a great difference in the total amount of flowering in the two study years. In 1967, most species flowered abundantly some time during the summer but in 1968 many flowered sparsely or not at all. In 1968, *Danthonia parryi*, *Festuca idahoensis* and *F. scabrella* did not flower at all in any of the areas studied.

Thus, in 1968 many species were far less conspicuous

than in 1967, and the appearance of these grasslands was considerably different.

The *Poa pratensis*-*Smilacina* Meadows (stands 2, 11, 17, 58, 59) are low-lying areas adjacent to the Waterton Lakes and the Waterton River. They are a mosaic of *Festuca-Danthonia* Prairie and the type of grass meadows represented by stands 9 and 60. Mesophytic hay-meadow grasses such as *Poa pratensis* and *Bromus pumpeiliianus* are more prominent in these areas than in the other *Festuca-Danthonia* Prairie stands, as are a number of other species, namely *Stipa columbiana*, *Geum triflorum*, *Lithospermum ruderales*, *Smilacina stellata* and *Vicia americana*.

2. Standing Crop

Three representative areas of *Festuca-Danthonia* Prairie were sampled for standing crop*: The first was a typical area in the Badlands adjacent to stand 64, which had not been subjected to much disturbance or grazing. The standing crop values from each set of five cones were averaged and Student "t-tests" were carried out to determine if there were any significant differences in mean standing crop on the two sampling dates, July 31 and August 27. The mean values were as follows: 1,118, 637, and 1,755 kg/ha for graminoids, forbs and total flowering plants respectively on July 31, and 977, 888 and 1,865 kg/ha respectively on August 27. Student t-tests indicated

* Standing crop = living, above-ground biomass.

that these differences were not significant at the 5% level (Table 5). Therefore, the values for the two dates were combined to give mean above-ground standing crop values for graminoids of 1,047 kg/ha, forbs 762 kg/ha and total flowering plants 1,809 kg/ha. There was a wide variation in standing crop from cone to cone, although the site was chosen for its uniformity. Total standing crop varied from 1,260 to 2,344 kg/ha. With so wide a variation and only 10 sample units only large differences in mean standing crop were significant at the 5% level. Most of the standing crop at this site consisted of the following species: *Danthonia parryi*, *Festuca scabrella*, *F. idahoensis*, *Carex* spp., *Galium boreale* and *Lupinus sericeus*.

The second site, at Upper Stoney Creek adjacent to stand 19, was an area of *Festuca-Danthonia* Prairie which had been heavily grazed by elk in winter and early spring. As with the Badlands site, t-tests showed no significant difference between standing crop on the two sampling dates, July 31 and August 27 (Table 5), and the results were therefore combined to give mean standing crop values of 776 kg/ha for graminoids, 632 kg/ha for forbs and 1,408 kg/ha for total flowering plants. Although the total flowering plant crop here was significantly less at the 5% level than that at the Badlands site, ($t = 2.65$), the separate values for graminoids and forbs were not (graminoids, $t = 1.77$; forbs, $t = 1.03$). The long-term effects of grazing by elk were

TABLE 5. STANDING CROP (kg/hectare) AT SEVEN GRASSLAND SITES IN 1968.

Site	July mean	August mean	t ¹	Combined means
Badlands, Waterton	July 31	August 27		
Graminoids	1118	977	0.5424	1047
Forbs	637	888	1.3135	762
Total	1755	1865	0.4497	1809
Upper Stoney Creek, Waterton	July 31	August 27		
Graminoids	751	802	0.2601	776
Forbs	759	506	1.8531	632
Total	1510	1308	1.0774	1408
Hay Meadow, Waterton	July 30	August 28		
Graminoids	1462	1254	0.3714	1358
Forbs	1038	682	1.2055	860
Total	2500	1936	0.7680	2218
Henry House, Jasper	July 14	August 20		
Graminoids	450	543	1.3719	497
Forbs	189	186	0.0624	188
Total	639	729	1.3349	685
Airstrip, Banff	July 16	August 23		
Graminoids	935	1084	0.6895	1010
Forbs	432	480	0.2330	456
Total	1367	1564	1.8130	1466
Tyrrell Creek, Banff	July 16	August 21		
Graminoids	590	827	3.4732**	
Forbs	285	296	0.0960	
Total	875	1123	1.6674	
Hillsdale Meadow, Banff	July 15	August 22		
Graminoids	1533	2279	2.2413*	
Forbs	281	299	0.2027*	
Total	1814	2578	2.6519	

FOOTNOTE. ¹Student "t-test" between July and August means; values of "t" attaining a 5% level of significance with 4 degrees of freedom (t=2.776) indicated as **, 10% level (t=2.132) as *.

probably indirectly responsible for the lower standing crop value obtained from these protected cones in the second site.

The species which contributed most to the standing crop at this site were *Danthonia parryi*, *Festuca idahoensis*, *Carex* spp., *Lupinus sericeus* and *Monarda fistulosa* var. *menthaefolia*.

The third site was a *Poa pratensis*-*Smilacina* Meadow in the vicinity of stand 59 in the Hay Meadow area. There was no significant difference in standing crop on July 30 and August 28, and the results were combined to give mean values of 1,358, 860 and 2,218 kg/ha for graminoids, forbs and total flowering plants respectively. These mean values were higher than those of the Badlands or Upper Stoney Creek sites but t-tests indicated that the differences were not significant at the 5% level. The apparent uniformity of this grassland was very deceptive, as the total standing crop of cones varied from 700 to 3,983 kg/ha. The major contributors to the standing crop at the Hay Meadow site were *Festuca idahoensis*, *Koeleria cristata*, *Poa pratensis*, *Carex* spp., *Lupinus sericeus*, *Monarda fistulosa* var. *menthaefolia* and *Smilacina stellata*.

Before the apparent differences in the standing crops of these three sites could be confirmed, sampling would have to be much more extensive to give a representative sample of such widely varied sites.

The rainfall during August, 1968 at Waterton Park H.Q.

was 1.85 inches higher than the long-term average of 1.96 inches (D.O.T., Met. Branch). Thus, there was not the usual period of drought, and the standing crop in late August did not, therefore, differ significantly from that of late July. The summer of 1967 was much drier, and it is probable that the standing crop for that year would have been significantly higher in July than in August.

3. Topography

The *Festuca-Danthonia* Prairie stands varied in elevation from 4,190 ft in No.2, *i.e.*, close to the lowest point in Waterton Lakes Nation Park, to 5,130 ft in No. 16. The upper altitudinal limit of this grassland type was not determined as there were some small areas of unsampled grassland at higher elevations, mostly on S-facing slopes in the Blakiston Brook valley. When corrected for latitude (p. 83), the mean elevation of the *Festuca-Danthonia* Prairie stands was the lowest in this study.

The stands of this grassland type sampled were on the glacial tills of ground moraines, eskerine complexes and drumlins (No. 1, 6, 7, 12, 14, 16, 17, 20, 64-71), on flat alluvium in river valleys (Nos. 2, 3, 11, 18), on relatively flat alluvial fans (Nos. 5, 8, 13, 15, 19, 58, 59, 62, 63) and on stabilised colluvial material (No.4) (Horberg, 1954).

Fourteen of the stands were on level ground and fifteen were on gentle slopes ranging from 1° to 8° and on all aspects. Stand No. 4 had a slope of 30° and represented extensive areas of intermittent and often shrubby grassland on the S-facing slopes of the Blakiston Brook and Waterton River valleys.

The largest area of *Festuca-Danthonia* Prairie is in the Badlands, being an area of six square miles of gently-rolling ground moraine, eskerine complexes and drumlins, which form a bench overlooking the west side of the Waterton River valley.

4. Soils

In the summary and comparison of soils data, some horizon data (Appendix 9, p. 330) are condensed to one value for each profile. This value is either the weighted mean of the mineral horizons or the value at the depth considered most meaningful, whichever is more appropriate (Table 6).

All the *Festuca-Danthonia* Prairie soils were Chernozems, although many had atypical features such as very high gravel content, ill-defined B horizon, and disturbed A horizon due to heavy grazing by elk. The thickness of the A horizon varied from 8 cm in the more xeric (No. 13) and heavily grazed (No.5) stands to 30 cm or more in the more mesic stands. It is unfortunate that soil identifications were not made in the field and

TABLE 6. PHYSICAL AND CHEMICAL PROPERTIES OF THE SOIL.

Stand	Sampling Date	Gravel ¹ %	Percentages in 0-2 mm fraction			Soil ^{1,2} tex- ture class	Depth ³ of top- soil in cm	moisture at 23 cm on sampling date	At 23 cm depth (%)			Available nutrients at 8 cm in			pH at 8 cm	pH at 70 cm	Free ⁶ lime at 8 cm	Free ⁶ lime at 60 cm
			sand ¹	silt ¹	clay ¹				Field Capa- city	Perm. Wilt- ing	Moisture Avail- ability	N	P	K				
1967																		
1	June 13	31	60	30	10	SaL	20	30.7	17.0	5.3	11.7	14½	7½	165	6.2	6.3	Nil	Nil
2	15	38	78	19	3	LSa	10	16.4	11.0	5.7	5.3	1½	3½	131	7.5	7.8	L	M
3	16	52	81	15	4	LSa	28	28.8	22.0	8.1	13.9	5½	3½	116	6.7	7.5	Nil	L
4	17	49	88	9	3	Sa	15 ⁴	10.9	7.9	5.0	2.9	1	5	138	6.3	6.14	Nil	Nil
5	18	43	82	12	6	LSa	10	23.4	18.3	8.6	9.7	9½	5	162	6.9	7.8	Nil	Nil
6	29	59	82	15	3	LSa	18	12.9	35.4	4.3	31.1	3½	7	151	6.9	8.0	Nil	M
7	July 1	79	90	7	3	Sa	5	8.3	28.4	9.0	19.4	½	8½	168	6.2	7.8	Nil	M
8	2	36	88	9	3	Sa	10	8.9	10.8	5.3	5.5	1	8½	218	7.2	7.6	L	Nil
9	3	2	62	32	6	SaL	30	24.9	25.8	15.1	10.7	20½	3½	137	6.9	8.0	Nil	T
10	3	3	54	39	7	SaL	20	34.5	26.5	8.9	17.6	24½	1	91	7.8	8.1	L	L
11	5	78	64	28	8	SaL	23	13.2	21.1	7.7	13.4	1	4½	174	6.1	7.2	Nil	Nil
12	26	12	32	40	28	CL	13	8.7	23.2	12.0	11.2	1½	2½	262	6.2	6.0	Nil	Nil
13	27	26	82	14	4	LSa	5	3.0	11.9	4.2	7.7	2	7½	153	7.2	8.0	Nil	T
14	28	39	81	14	5	LSa	13	7.2	11.2	6.7	4.5	4	6	152	6.3	7.6	Nil	Nil
15	29	51	58	30	12	SaL	36	9.5	26.6	12.9	13.7	½	2	118	6.2	7.6	Nil	T
16	30	22	49	28	23	SaCL	30	10.7	32.8	11.7	21.1	½	6	300+	6.1	6.4	T	Nil
17	30	0	56	32	12	SaL	30	7.8	16.3	8.0	8.3	1	1	216	7.2	7.6	Nil	M
18	31	60	85	11	4	LSa	30	5.5	13.8	9.5	4.3	1½	7	177	6.0	6.8	Nil	T
19	Aug. 1	64	79	17	4	LSa	5	5.3	16.2	8.9	7.3	2	13	300+	6.2	7.4	Nil	T
20	2	54	77	18	5	LSa	25	5.6	29.9	24.1	5.8	2½	11	294	6.0	6.0	Nil	Nil
21	June 20	65	82	12	6	LSa	8	28.4	20.5	5.6	14.9	8½	3	110	7.6	8.1	L	H
22	21	8	51	38	11	L	20	41.2	19.2	11.2	8.0	6	5	89	7.8	8.3	L	H
23	July 7	80	87	8	5	LSa	10 ⁴	1.4	6.2	1.9	4.3	2	7½	144	6.7	7.8	Nil	M
24	8	79	63	31	6	SaL	10 ⁴	21.6	55.5	43.0	12.5	2½	15½	272	7.2	7.5	Nil	L
25	9	7	46	44	10	SaL	20	26.1	36.5	20.4	16.1	9½	3	106	7.4	8.0	M	M
26	10	62	48	47	5	SaL	46 ⁴	18.6	50.5	30.4	20.1	1½	9½	174	7.4	8.0	Nil	L
27	11	53	76	21	3	LSa	18	3.6	7.0	2.8	4.2	0	2½	227	7.6	8.1	L	H
28	12	68	79	15	6	LSa	10	7.5	11.4	5.6	5.8	1	2½	90	7.4	8.1	T	H
29	Aug. 4	41	57	35	8	SaL	10	5.8	28.7	17.3	11.4	1½	6	212	6.7	6.8	Nil	Nil
30	5	6	52	34	14	L	13	18.3	33.2	20.5	12.7	12½	3½	300+	6.9	8.3	Nil	H
31	6	59	80	16	4	LSa	13	6.3	13.4	6.8	6.6	3	3½	126	7.4	8.0	Nil	M
32	8	66	72	23	5	SaL	8	8.6	22.4	11.1	11.3	3	2½	139	8.0	7.9	M	H
33	28	45	69	24	7	SaL	5	4.9	24.0	9.1	14.9	0	1	156	7.4	8.1	Nil	VH
34	29	0	21	48	31	CL	8	14.1	28.9	11.2	17.7	½	2	148	7.5	8.3	L	H
35	30	16	70	23	7	SaL	3	2.8	19.1	5.9	13.2	0	1	44	8.0	8.2	M	H
36	June 22	3	65	31	4	SaL	3	6.1	10.6	8.8	1.8	½	0	41	8.0	8.0	H	H
37	23	0	15	77	8	SiL	3	8.7	5.8	5.4	0.4	½	0	30	8.1	8.3	H	H
38	July 12	21	60	18	22	SaCL	5	2.3	5.3	1.9	3.4	1½	½	99	8.0	8.3	H	H
39	15	47	75	19	6	SaL	5	4.6	25.8	6.9	18.9	1	½	51	8.0	8.0	H	H

TABLE 6. PHYSICAL AND CHEMICAL PROPERTIES OF THE SOIL. (Cont'd.)

Stand	Sampling Date	Gravel ¹ %	Percentages in 0-2 mm fraction			Soil ^{1,2} tex- ture class	Denth ³ of top- soil in cm	Soil moisture at 23 cm on sampling date	At 23 cm depth (%)			Available nutrients at 8 cm in			pH at 8 cm	pH at 60 cm	Free ⁶ lime at 8 cm	Free ⁶ lime at 60 cm	
			sand ¹	silt ¹	clay ¹				Field Capa- city	Perm. Wilt- ing	Moisture Avail- ability	N	ppm P	K					
40	July	16	0	7	36	57	C	10	15.1	43.1	12.8	30.3	1	3½	161	5.5	5.9	Nil	Nil
41		16	1	59	17	24	SaCL	5	13.4	40.5	21.2	19.3	1	1	104	7.6	7.5	Nil	Nil
42		17	3	42	37	21	L	8	6.5	32.6	13.3	19.3	1	2½	300+	7.9	8.3	M	H
43		18	5	91	4	5	Sa	3	1.6	9.0	3.1	5.9	½	2	23	8.4	8.6	H	M
44		19	44	70	21	9	SaL	5	4.1	7.6	3.0	4.6	½	1	76	7.9	8.2	H	H
45	Aug.	9	29	69	26	5	SaL	10	11.3	25.1	10.5	14.6	3½	2½	158	8.0	8.3	H	H
46		10	0	21	48	31	CL	5	8.8	37.9	12.6	25.3	½	5	115	6.2	6.3	T	Nil
47		11	15	47	41	12	L	13	8.5	24.6	8.7	15.9	0	0	58	8.0	7.9	H	H
48 ⁵		12	9	43	48	9	SaL	3	10.4	25.1	9.9	15.2	3	1	68	7.9	8.4	H	H
49		13	0	87	6	7	Sa	3	2.8	4.9	2.0	2.9	3	1	80	7.9	8.4	H	M
50		19	43	43	37	20	L	15	14.1	30.8	7.7	23.1	0	3½	34	7.7	8.1	T	M
51		23	40	81	13	6	LSa	13	2.4	7.9	3.0	4.9	0	5	65	7.7	8.2	M	H
1968																			
52	June	14	0	81	14	5	LSa	10	11.0	11.6	5.0	6.6	½	0	105	8.0	9.1	H	H
53		14	0	85	10	5	LSa	10	9.5	8.1	3.1	5.0	½	0	76	8.1	8.6	H	H
54		15	4	90	7	3	Sa	5	4.1	5.8	1.9	3.9	½	2	109	8.4	8.5	H	M
55		16	4	89	7	4	Sa	6	3.8	6.4	2.0	4.4	½	4	107	8.2	8.6	L	M
56		17	0	88	7	5	Sa	5	2.2	5.6	1.8	3.8	1	2	222	8.5	8.7	M	L
57		18	6	87	8	5	Sa	6	4.2	6.6	1.9	4.7	½	½	142	8.5	8.9	H	M
58		22	3	69	24	7	SaL	18	18.8	16.5	7.4	9.1	2½	4½	234	6.9	7.8	Nil	Nil
59		22	11	66	26	8	SaL	18	22.2	15.8	6.3	9.5	5	3½	213	7.2	7.9	Nil	L
60		24	12	68	24	8	SaL	20	27.2	17.7	8.3	9.4	1½	4	187	6.8	8.0	Nil	T
61		24	13	77	15	8	LSa	13	28.2	14.8	6.6	8.2	1	2	84	8.0	7.8	L	Nil
62		26	64	92	5	3	Sa	5	7.0	7.1	4.2	2.9	2½	4	114	7.7	8.0	Nil	L
63		27	51	87	9	4	Sa	8	13.9	8.8	5.2	3.6	1	3	108	6.8	7.9	Nil	L
64		21	54	87	9	4	Sa	8	10.1	9.9	5.3	4.6	4	6	199	6.2	6.2	Nil	Nil
65	Aug.	2	66	82	14	4	LSa	10	10.4	13.0	7.1	5.9	3½	6	226	6.2	6.2	Nil	Nil
66		7	39	83	11	6	LSa	25	10.3	12.1	5.8	6.3	0	4½	170	5.5	5.8	Nil	Nil
67		8	59	86	10	4	LSa	8	8.0	13.1	6.4	6.7	½	5½	182	6.3	6.6	Nil	Nil
68		13	56	89	7	4	Sa	8	9.0	12.2	5.5	6.7	1½	7	201	6.1	7.2	Nil	Nil
69		14	34	59	31	10	SaL	8	10.5	18.5	6.0	12.5	0	4½	183	6.0	8.1	Nil	H
70		15	40	83	12	5	LSa	10	13.6	12.9	6.6	6.3	0	6	189	6.0	6.3	Nil	Nil
71		15	21	72	19	9	SaL	25	19.8	20.2	9.3	10.9	0	6	258	5.8	5.9	Nil	Nil

Footnotes: ¹ the weighted mean values of all mineral horizons down to 90 cm.

² Sa = sand, Si = silt, C = clay, L = loam, SaL = sandy loam.

³ topsoil includes both Ah and F-H horizons.

⁴ since a profile of loose, unweathered, angular rocks was intermixed with humus to considerable depths, this value is only approximate.

⁵ this stand had a very high concentration of sodium and sulphate ions and a high conductivity (3.4 mmhos) at depths below 25 cm.

⁶ T = trace, L = low, M = medium, H = high, VH = very high.

that little note was made of profile structure. These omissions made subsequent identifications in the laboratory rather tentative.

However, 18 of the soils appeared to be Orthic Black Chernozems, good exmples of which were Nos. 14, 18 and 20. The other 12 soils were tentatively identified as Orthic Dark Brown (Nos. 3, 58 and 59), Orthic Dark Grey (No. 15), Rego Black (Nos. 4, 5, 7, 13, 19, 68), and Rego Dark Brown Chernozems (Nos. 62, 63) (National Soil Survey Committee, 1968). The Rego Black and Rego and Orthic Dark Brown Chernozems were prevalent on the more xeric sites and on areas heavily grazed by elk.

The average textures of the mineral profiles (to 90cm) in 28 of the 30 soils were sands, loamy-sands or sandy-loams, and clay content was very low. (National Soil Survey Committee, 1968). The other two soils (Nos. 12 and 16) had 28% and 23% clay and were identified as clay-loam and sandy clay-loam respectively.

Potentially available moisture at Field Capacity varied from 31.1% in No. 6 to 2.9% in No.62. In order to compare field moisture determinations with soil constants such as Field Capacity (FC) and Permanent Wilting Point (PWP), it was necessary to take the sampling date into account by dividing the 18 stands sampled in 1967 into three groups, all stands within a group being sampled within a short time period. On the assumption that the stands were sampled on a random geographic basis, the average soil

moisture contents (the mean of five or more values in each stand at a depth of 23 cm) were calculated for each group to obtain an approximation of soil moisture deficits throughout the growing months.

Group 1. June 13 to 18, stands 1 to 5, mean moisture = 22.0%.

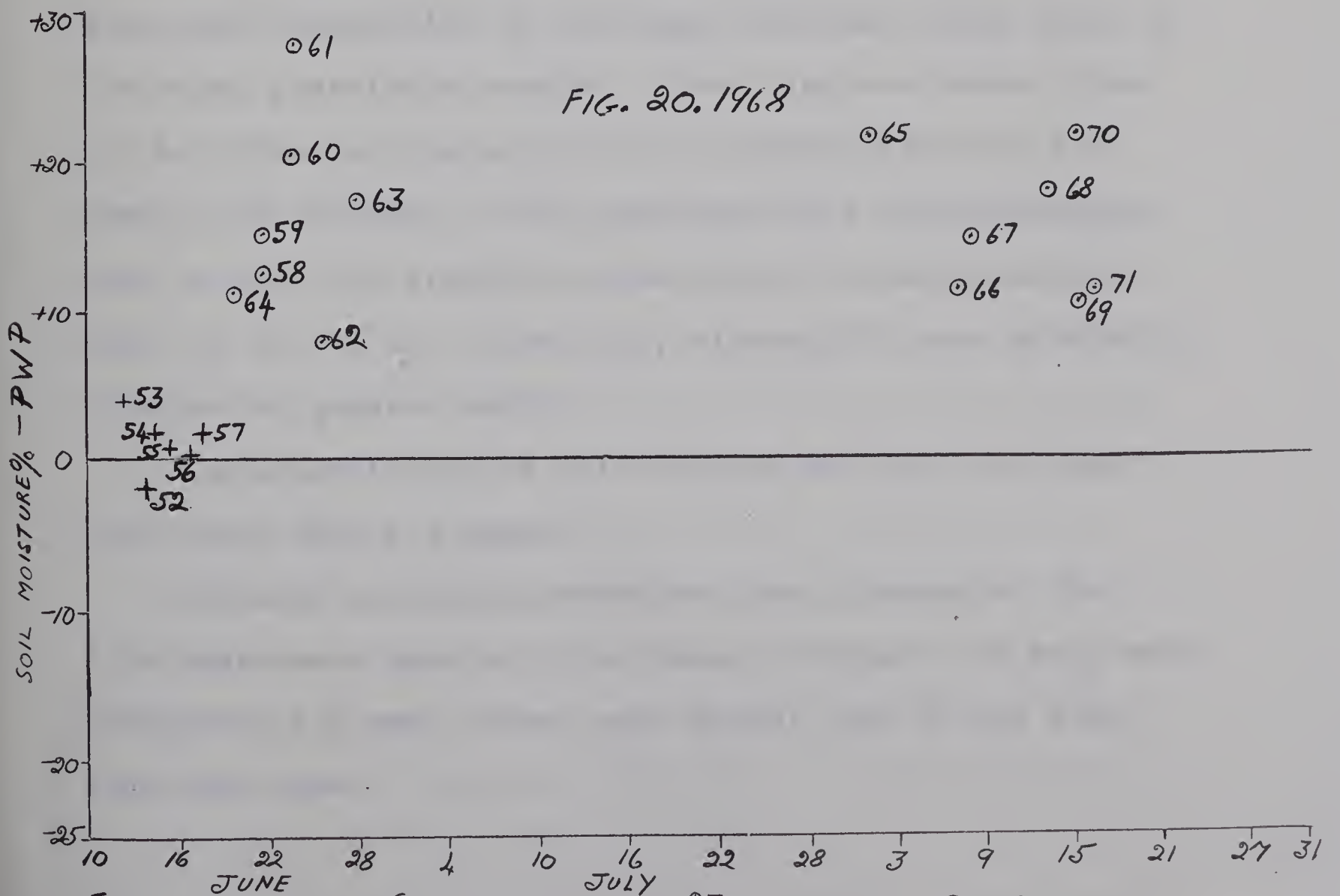
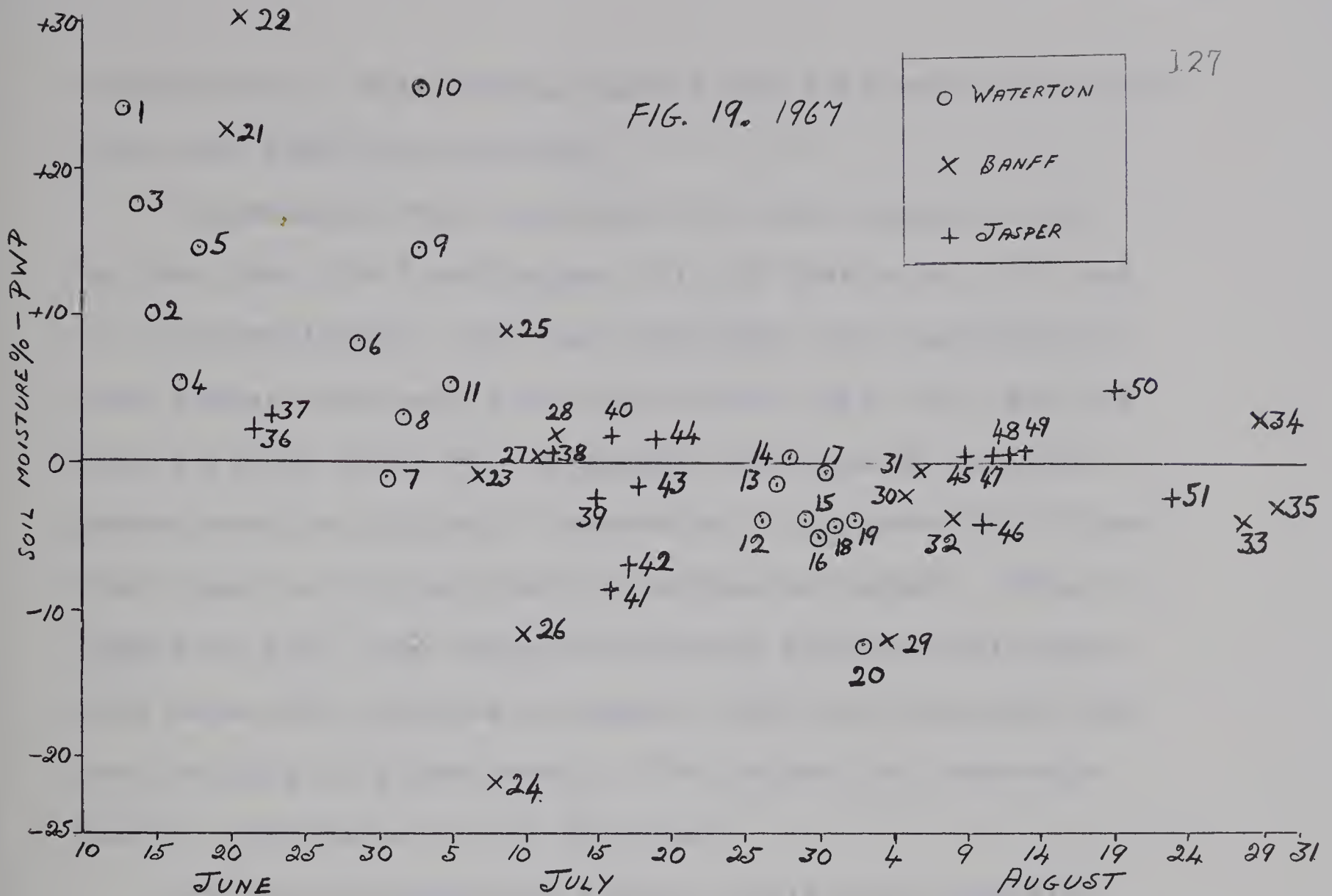
Group 2. June 29 to July 5, stands 6 to 8 and 11, mean moisture - 10.8%.

Group 3. July 26 to August 1, stands 12 to 20, mean moisture - 7.0%.

When the individual moisture contents are compared with FC and PWP, it can be seen (Fig. 19) that in Group 1 all five soils were above FC. In Group 2, all four soils were below FC and the moisture in one of them (No.7) had dropped below the PWP. In Group 3, all of the nine soils except No. 14 had dropped below the PWP. Hence, by the end of July 1967, most of the *Festuca-Danthonia* Prairie was desiccated, and above-ground growth of most species had apparently ceased, although many of the composites did not flower until the middle of August.

The summer of 1967 was unusually dry, with 6.36, 0.41 and 0.77 inches of rainfall in June, July and August respectively at Waterton Lakes Ranger Station. These values were 1.46 inches above normal for June but 1.44 inches and 1.19 inches below normal for July and August (Can. Dept. Transport, 1967).

The summer of 1968 was much wetter, with 4.98, 3.43 and 4.67 inches of rainfall in June, July and August



FIGS. 19 AND 20. SOIL MOISTURE AT 23 CM DEPTH IN RELATION TO PERMANENT WILTING PERCENTAGE ON THE DATE OF SAMPLING.

respectively. These values were 0.08, 1.58 and 2.71 inches above the long-term averages.

The mean moisture contents of soils sampled in the periods June 21-27 and August 2-15 of 1968 were 19.0% and 25.2% respectively. All the individual soil moistures in both groups were well above their PWP's (Fig. 20), and all were slightly above FC. Although the soils of the two groups were not strictly comparable, it appears that there was a gain in soil moisture from June to August. Thus, by August of 1967, the *Festuca-Danthonia* Prairie soils were well below PWP, whereas in August, 1968 soil moisture was not limiting to plant growth. The values for June were roughly comparable in the two years.

The *Festuca-Danthonia* Prairie soils were generally more acid, especially in the upper horizons, than those of the other grasslands sampled. Free lime was absent from all but three of the soils at 8 cm depth and from 17 of them at 60 cm depth. Soil reactions were correspondingly low; in only six stands was the pH at 8 cm above neutral (Nos. 2, 8, 13, 17, 59 and 62), although 20 were distinctly alkaline at greater depth.

The conductivity of all horizons was very low and never more than 0.4 mmhos.

Although available phosphorus and nitrogen at the 8 cm depth were generally low (mean nitrogen = $2\frac{1}{2}$ ppm, mean phosphorus = 6 ppm) values were higher than in the other grassland types.

There was no deficiency of available potassium in any stand, high values being recorded in nearly all horizons. Available potassium reached a maximum in these soils, with a mean value of 190 ppm at 5 cm depth.

To sum up, a typical soil from this grassland type would be a Chernozem with about 25 cm of black-dark brown topsoil; a moderately high gravel content and an Available Water Capacity of 5-10% in the loamy-sand, mineral horizons; free lime and slightly alkaline pH values in the B and C horizons but little free lime and low pH values in the A horizons; very low conductivity, available nitrogen and phosphorus in the topsoil, but high available potassium values.

5. Ordination of the *Festuca-Danthonia* Prairie Stands

The *Festuca-Danthonia* Prairie stands had a high degree of similarity to the end stands 13 and 15 on the 51-stand ordination, but a low degree of similarity to the other four end stands. There was also a clear division between the *Festuca-Danthonia* Prairie stands and the other stands on the ordination. The inter-stand distances of this cluster were relatively small, thus making the 51-stand ordination somewhat inadequate as a basis for the study of vegetational and environmental variation within the grassland type.

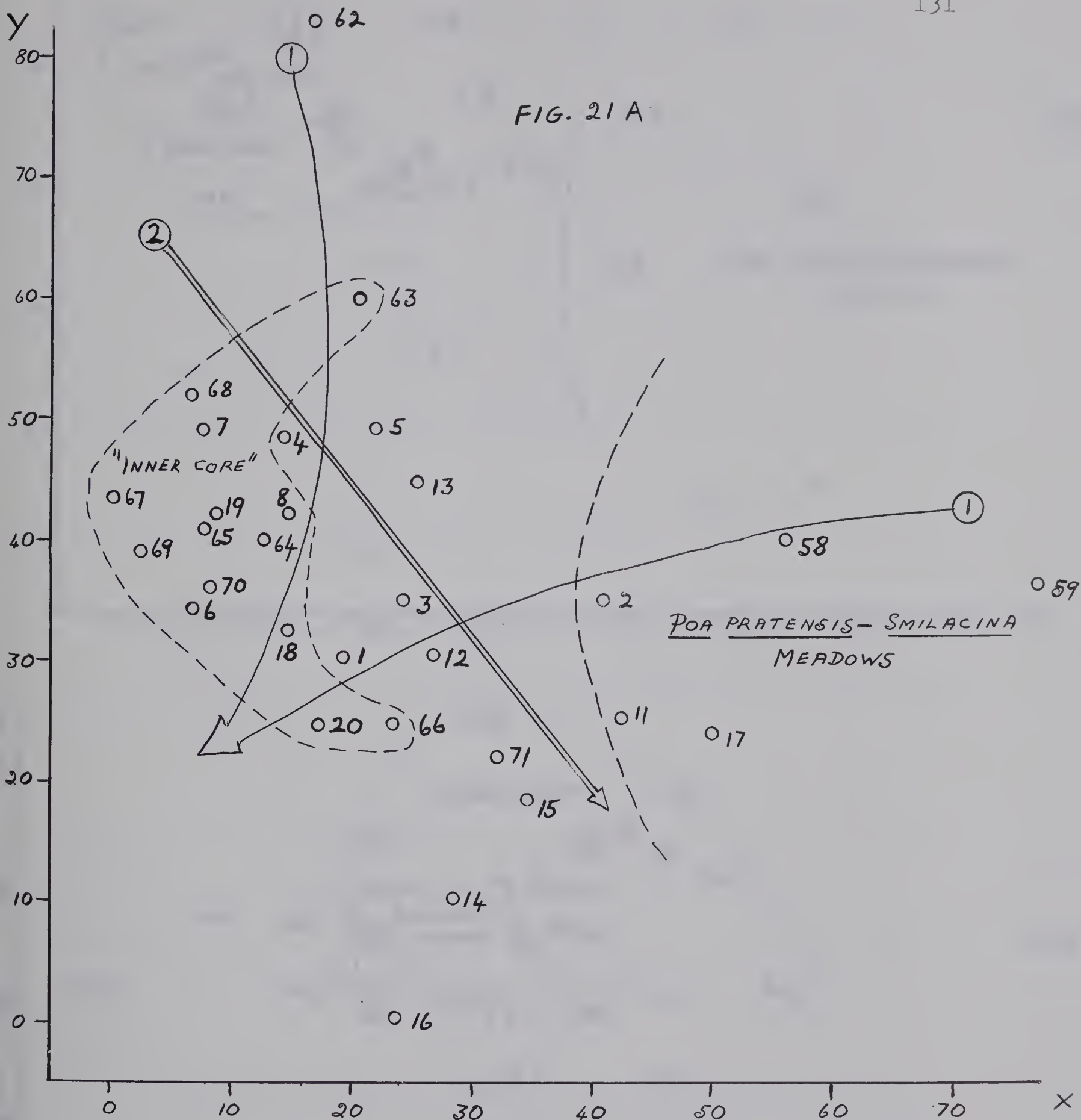
Therefore, a separate three-dimensional ordination

of the 30 *Festuca-Danthonia* Prairie stands was constructed in the same way as the 51-stand ordination (see p. 62-5). The end stands of the three axes were Nos. 67 and 59 for the X axis, Nos. 15 and 62 for the Y axis, and Nos. 1 and 18 for the Z axis. The lengths of the X, Y and Z axes were 76.8, 81.3 and 53.7 units respectively.

The positions of the 30 stands were plotted in the three principal planes of the ordination, with the values of X, Y and Z of each stand as co-ordinates (Appendix 8, p. 327; Fig. 21).

As before, it was considered necessary to determine the validity of the new 30-stand ordination and, in addition, to assess its improvement, if any, upon the 51-stand ordination. Fifty pairs of stands were chosen at random and simple correlation coefficients calculated between their "Dissimilarity values" ($100 - \text{Index of Similarity}$) and the actual distance apart on the two ordinations. The "r" value of the IS/30-stand ordination was + 0.7430 for the XY plane and + 0.7414 for the three-dimensional XYZ ordination, both being significant at the 1% level, compared with "r" = + 0.5504 and 0.6782 respectively for the IS/51-stand ordination. It is concluded that the separate ordination represents more adequately the vegetational relationships between the 30 *Festuca-Danthonia* stands, especially when only the XY plane is considered.

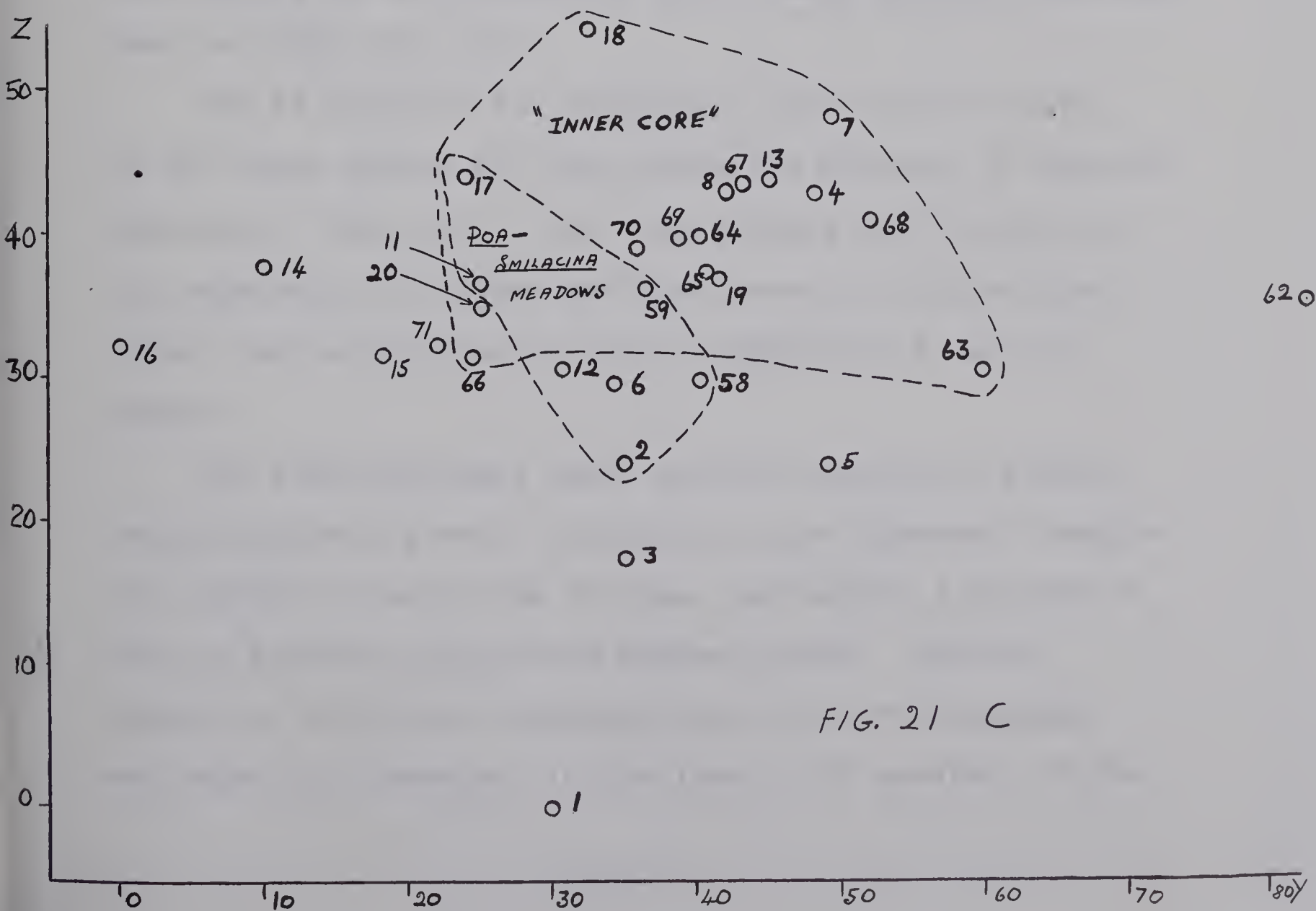
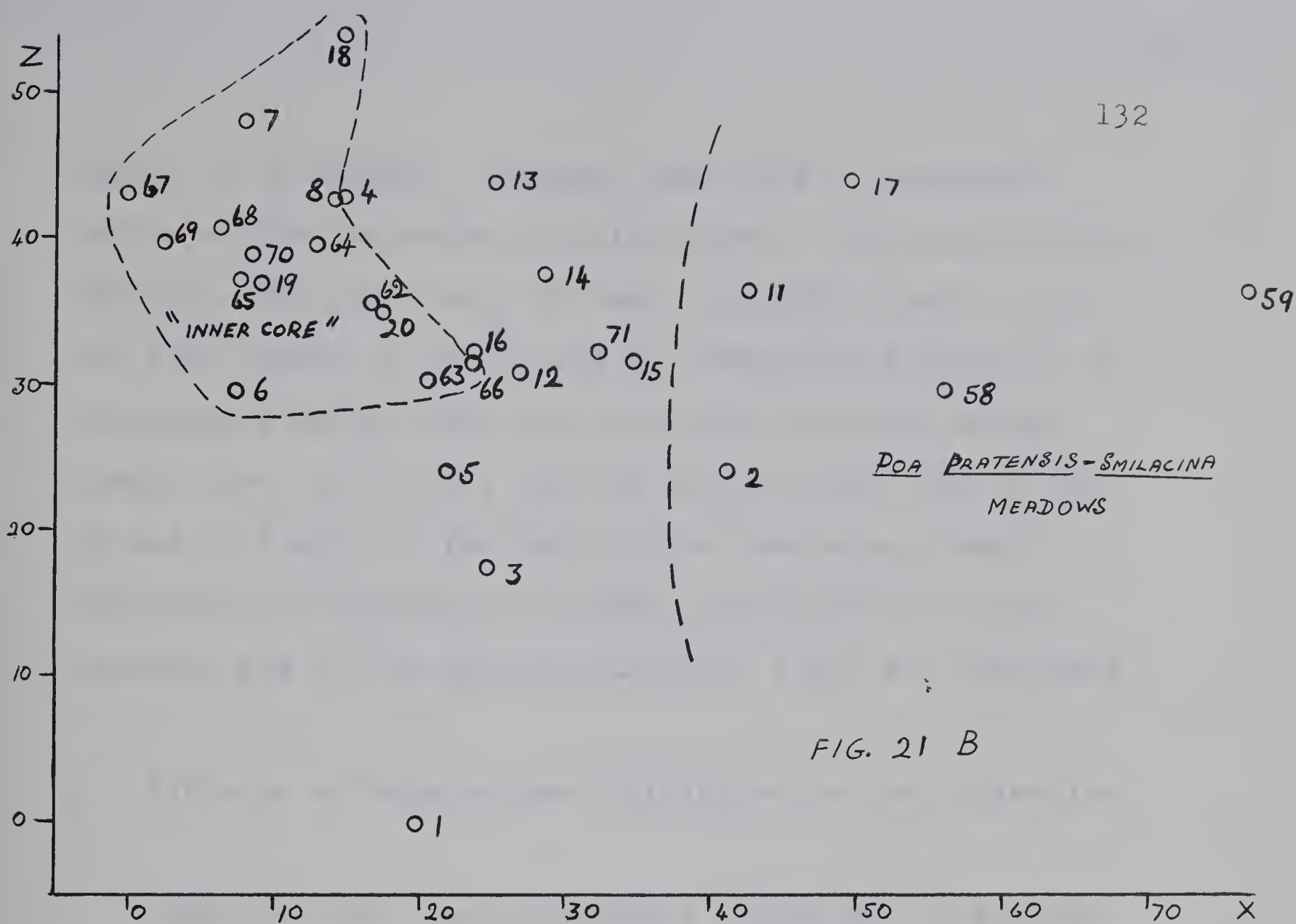
Inspection of the improved ordination made it evident that there are no marked vegetational discontinuities



The location of stands on the 30-stand Festuca-Danthonia Prairie ordination.

- A. on the XY plane.
- B. on the XZ plane.
- C. on the YZ plane

Poa pratensis-Smilacina Meadow stands (Nos. 2, 11, 17, 58, 59), and the "inner core" stands of the Festuca-Danthonia Prairie (Nos. 6-8, 18-20, 63-70) enclosed with broken lines. Trends 1 and 2 as described on p. 143 indicated with arrows.



among the 30 stands. Instead, they form a continuous series within one major grassland type - *Festuca-Danthonia* Prairie. The inner core of "most typical" stands is in the left centre of the XY and XZ ordination fields; it is separated from the five *Poa pratensis-Smilacina* Meadow stands (Nos. 2, 11, 17, 58, 59) at the right side of the XY and XZ fields by the bulk of the remaining stands. Thus, the configuration of stands indicated by cluster analysis and by the phytosociological table was confirmed.

6. Patterns of Vegetational Attributes on the Ordination

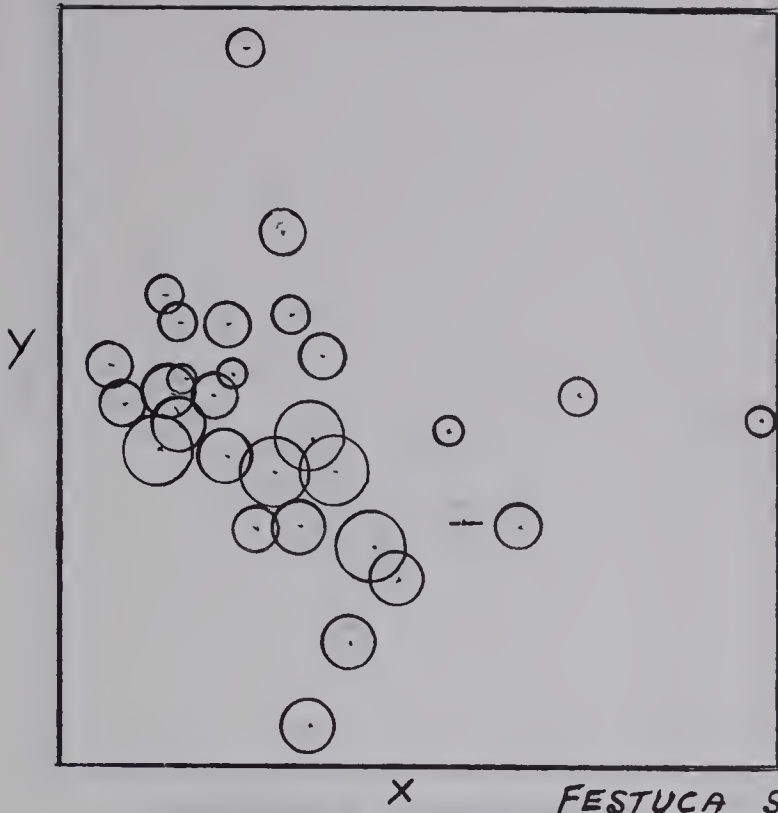
When the mean Cover-abundance values of the species are plotted on the ordination field, many distinct patterns come to light (Fig. 22).

The XY plane of the ordination was the most useful of the three planes for describing the patterns of species abundance. The short Z axis contributed very little to the separation of stands and there were no distinct patterns, the description of which required the XZ and YZ planes.

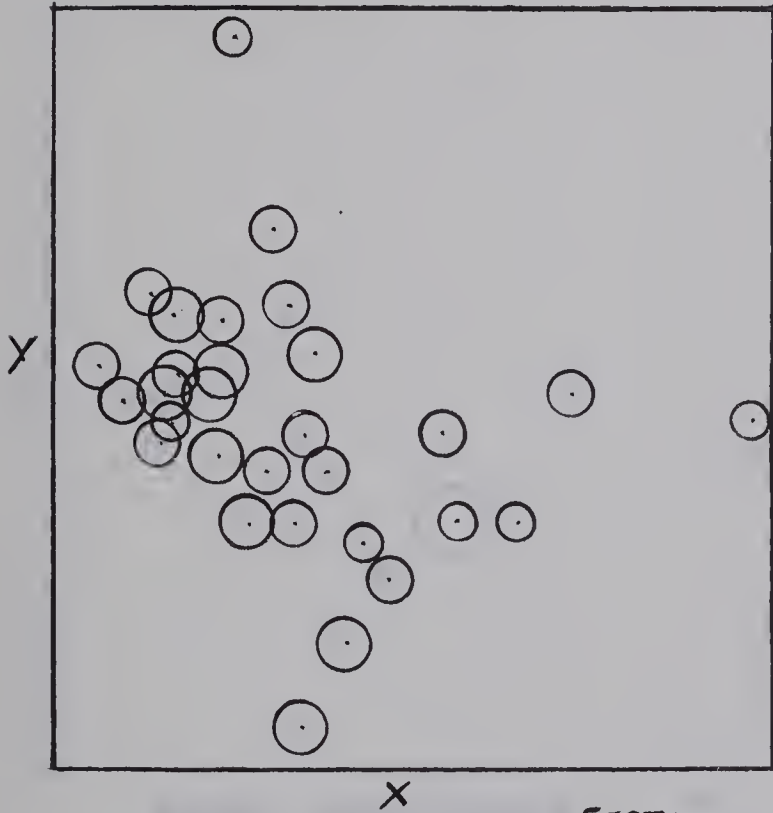
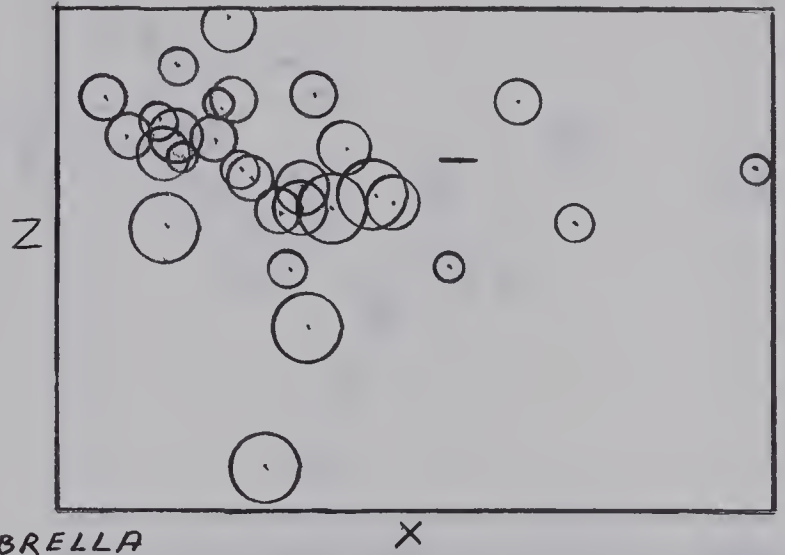
The three Dominant bunch grasses—*Danthonia parryi*, *Festuca scabrella* and *F. idahoensis*—are abundant throughout the left side of the XY plane and are at a minimum in the *Poa pratensis-Smilacina* Meadow stands. *Festuca scabrella*, *Danthonia intermedia* and *Stipa richardsonii* are especially abundant in the lower left quadrant of the

Figure 22. The distribution patterns of three species on the XY and XZ planes, and 18 species on the XY plane of the 30-stand *Festuca-Danthonia* Prairie ordination.

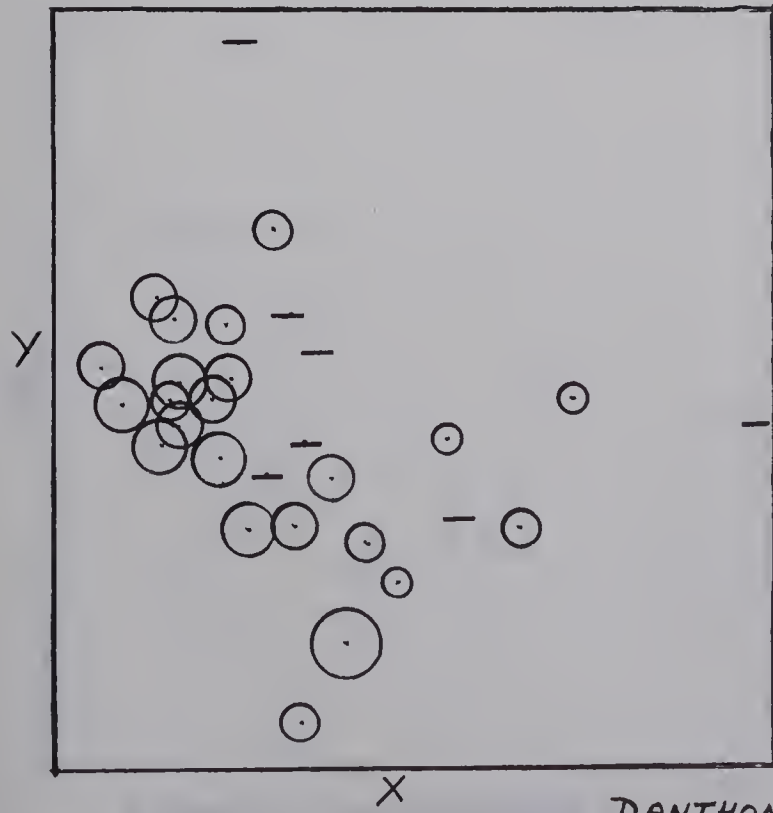
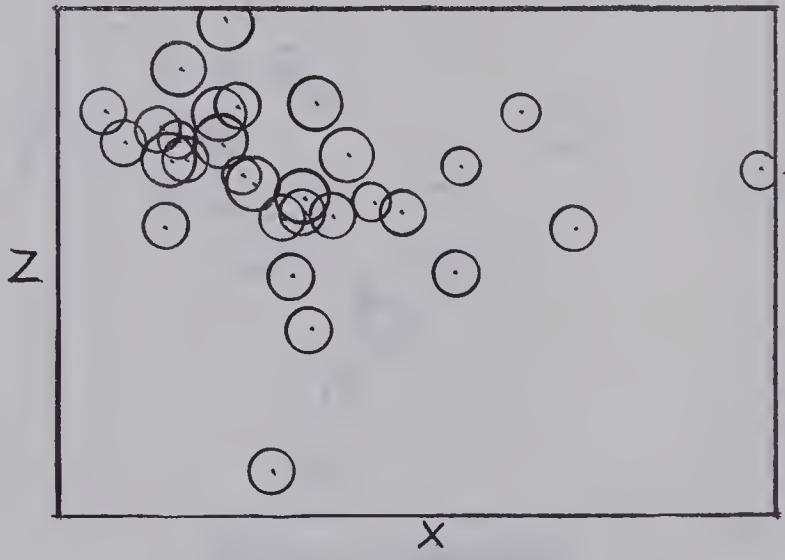
Progressively larger circles represent Cover-abundance values of P, +, 1, 2, 3, 4 and 5; absence from a stand represented by a dash.



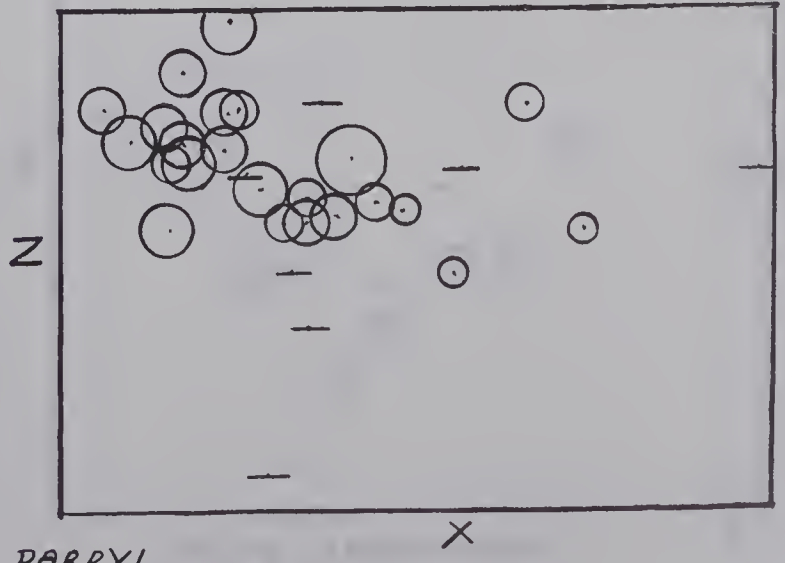
FESTUCA SCABRELLA

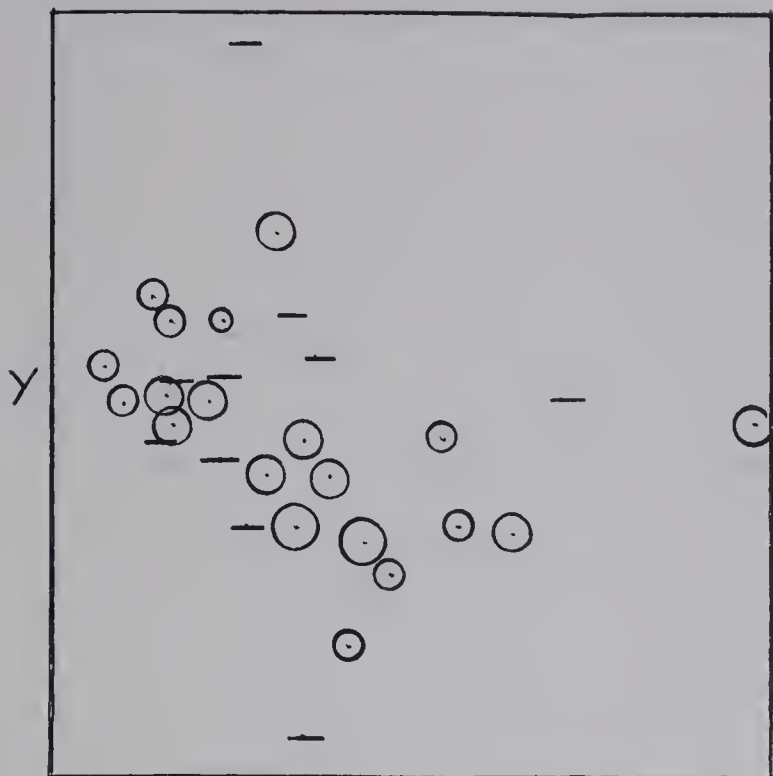


FESTUCA IDAHOENSIS

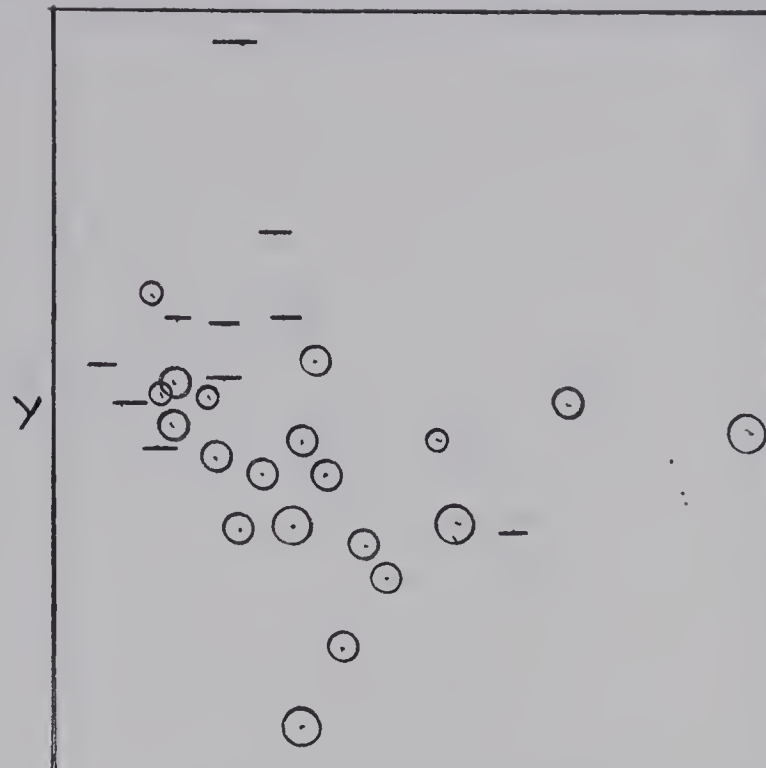


DANTHONIA PARRYI

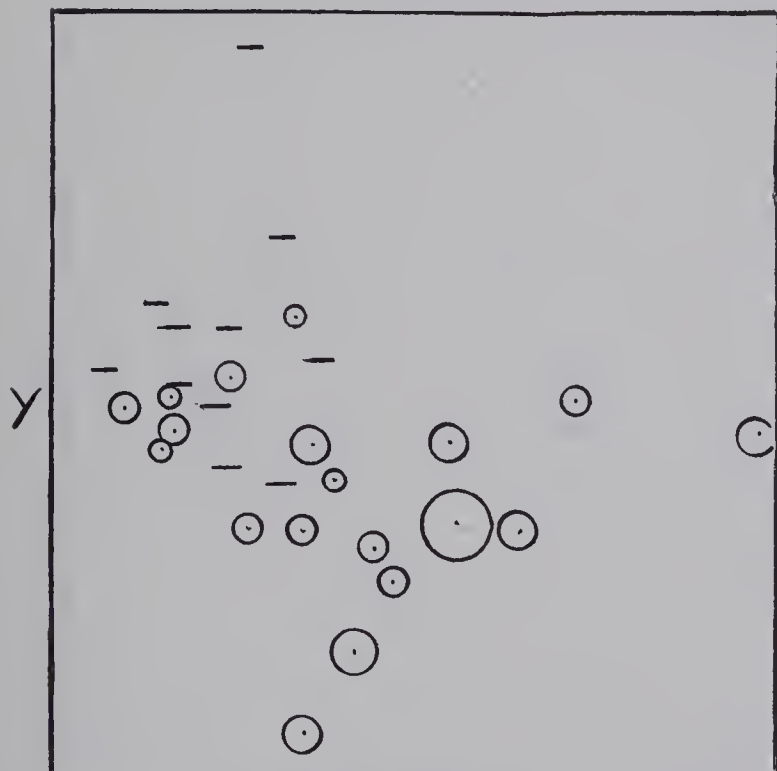




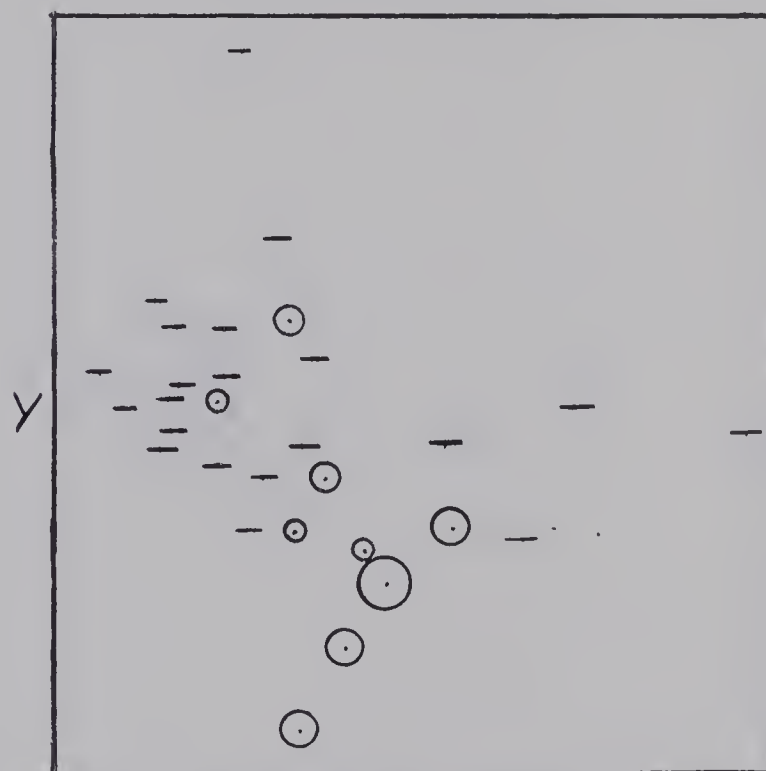
DANTHONIA INTERMEDIA X



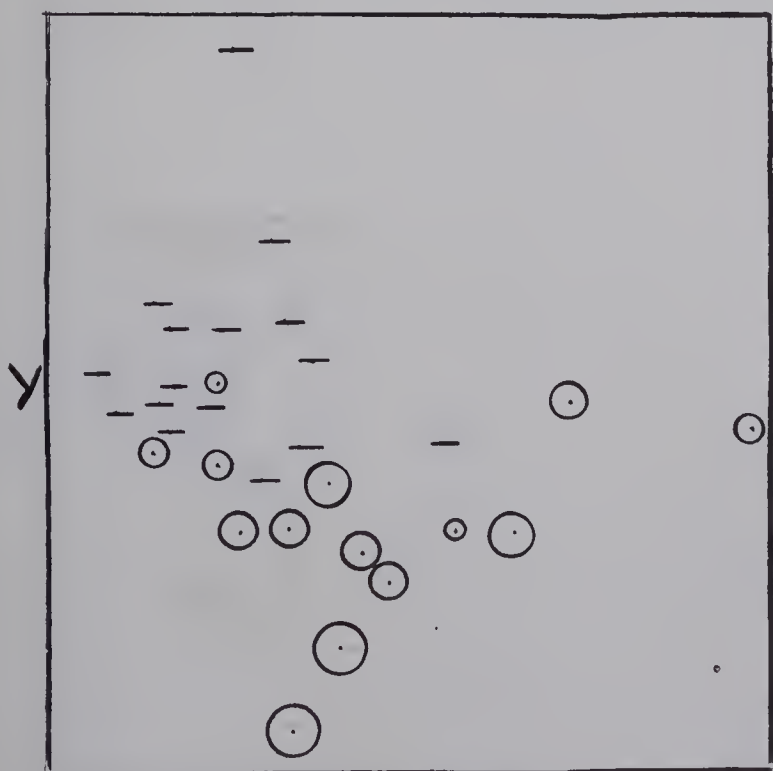
AGROPYRON TRACHYCAULUM VAR. *UNILATERALE* X



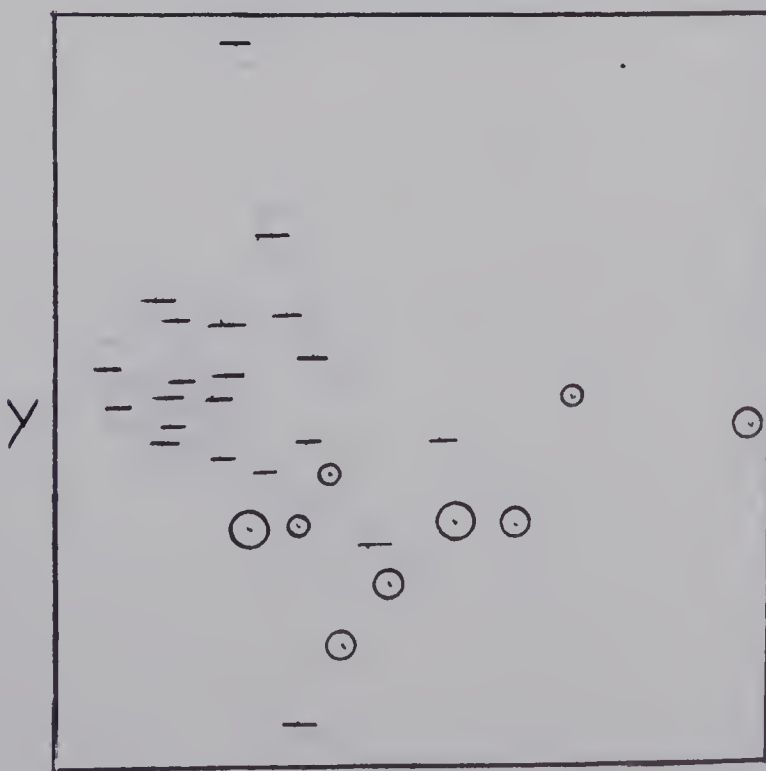
BROMUS PUMPELLIANUS X



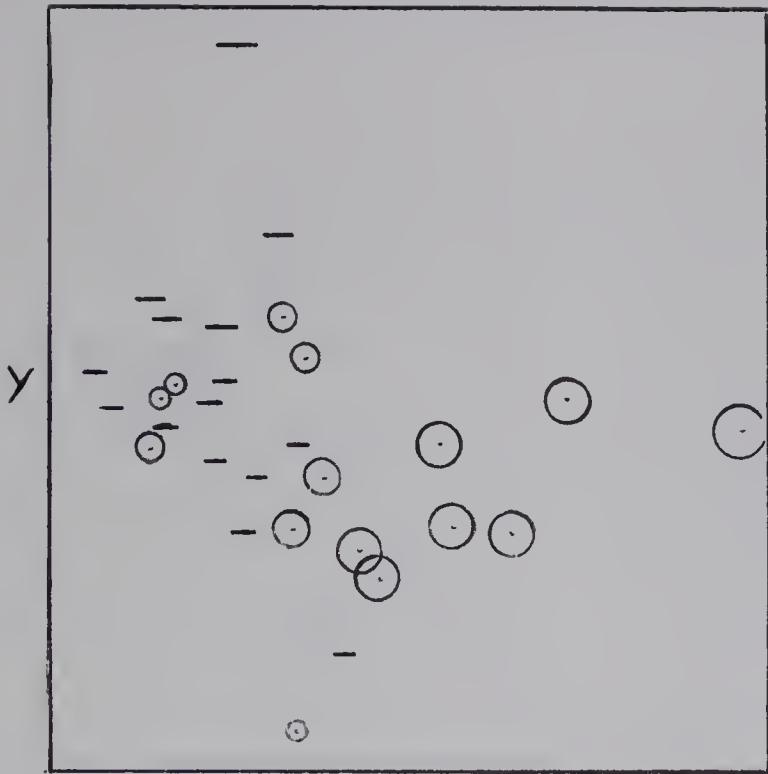
PHLEUM PRATENSE X



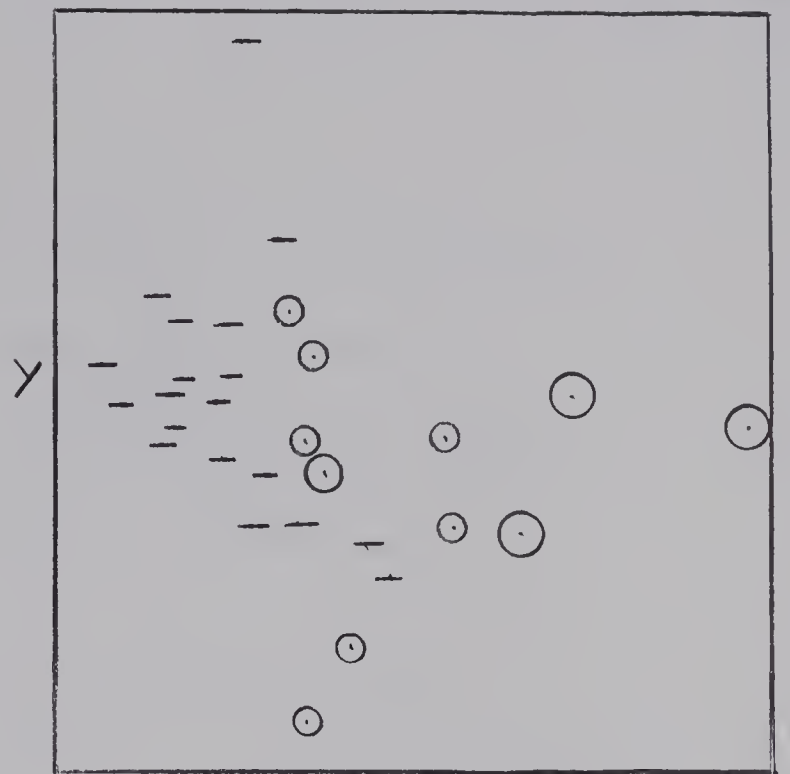
GERANIUM VISCOSISSIMUM X



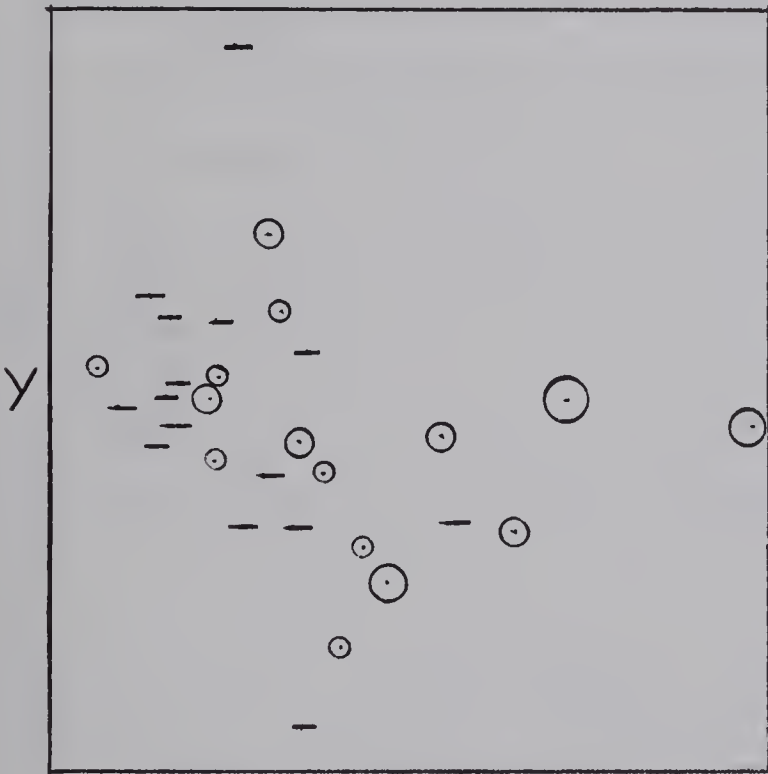
VICIA AMERICANA X



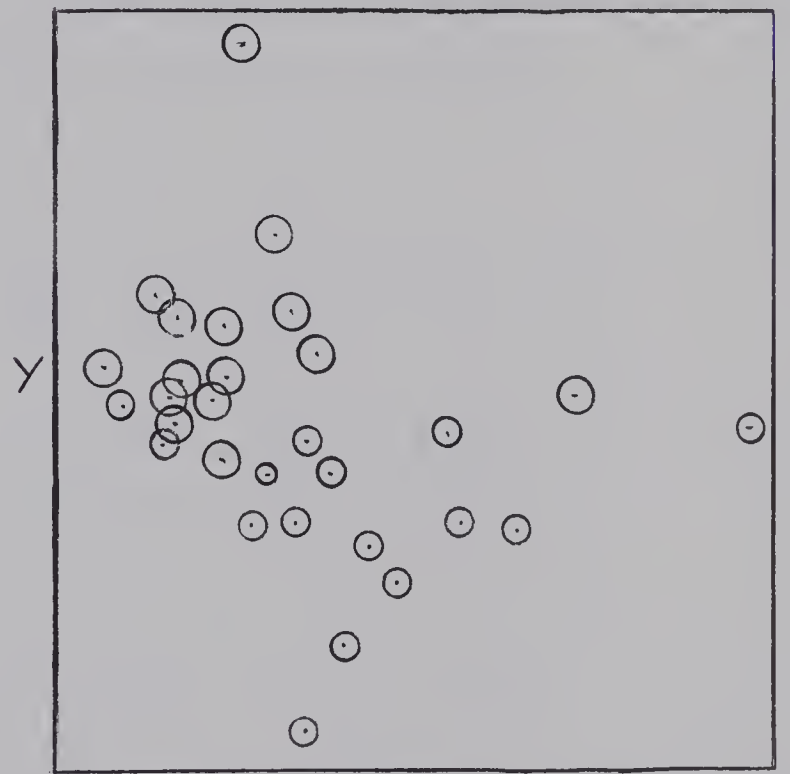
POA PRATENSIS



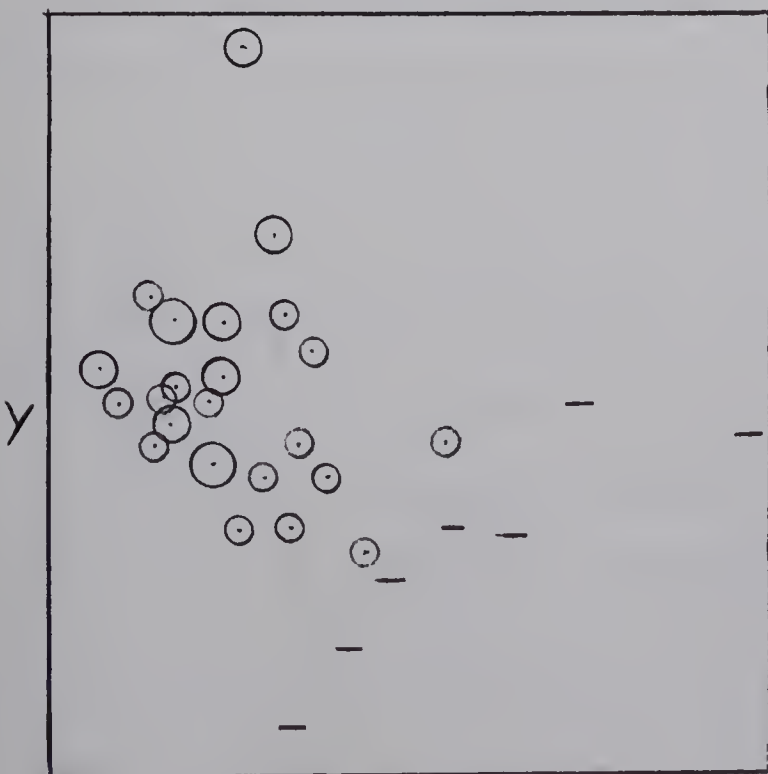
SMILACINA STELLATA



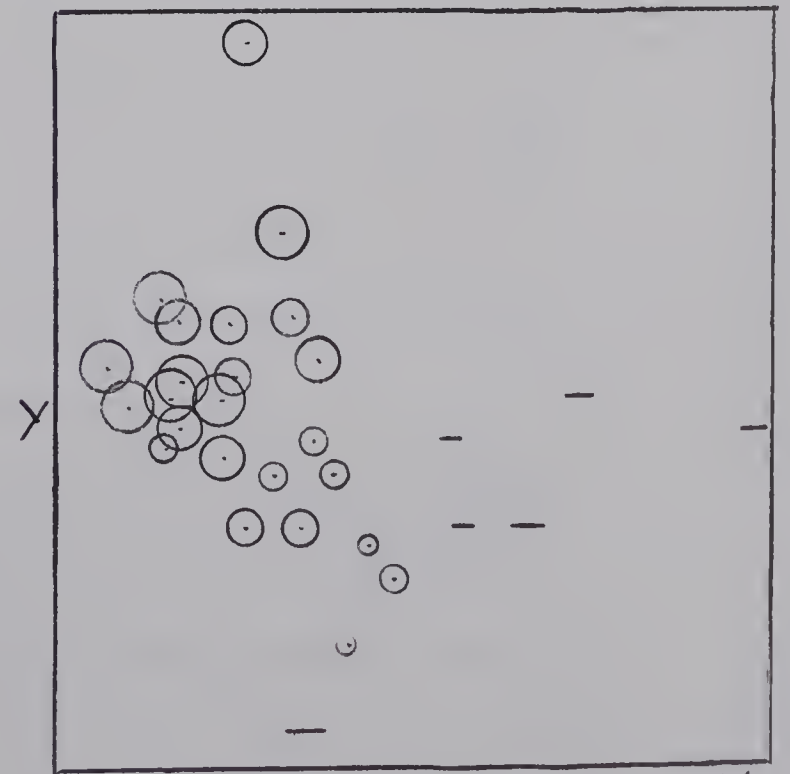
GEUM TRIFLORUM



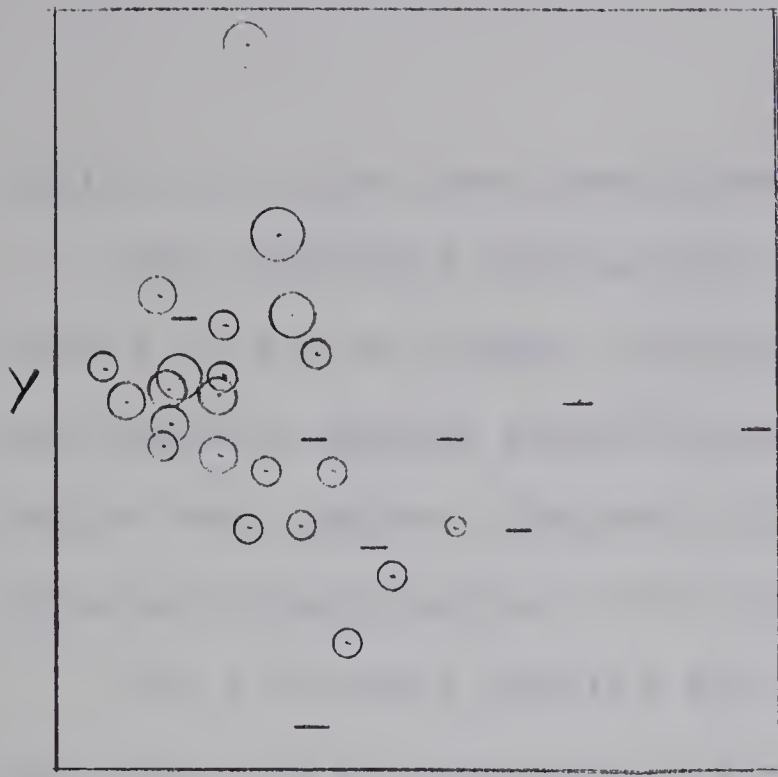
KOELERIA CRISTATA



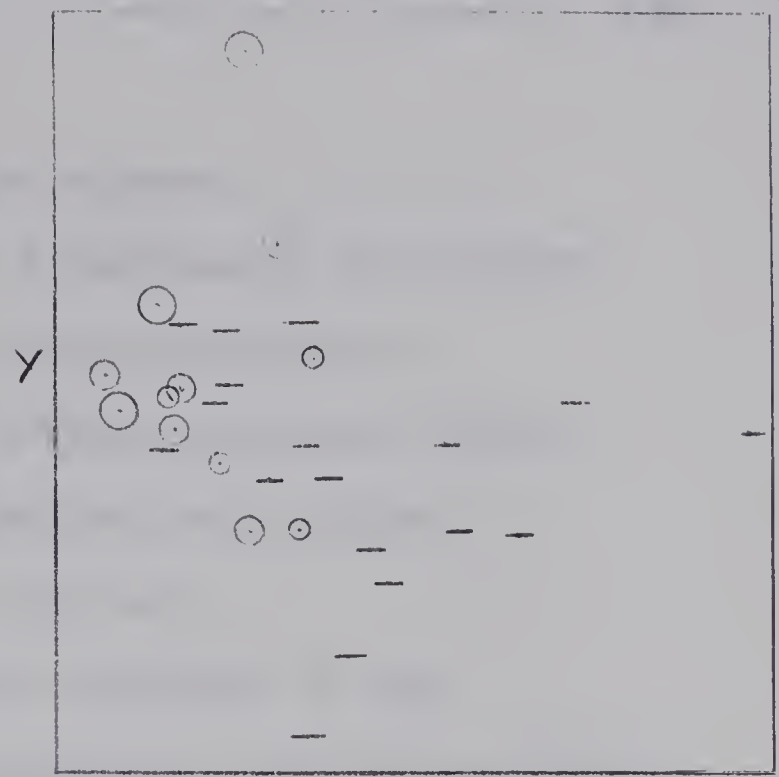
ANTENNARIA UMBRINELLA



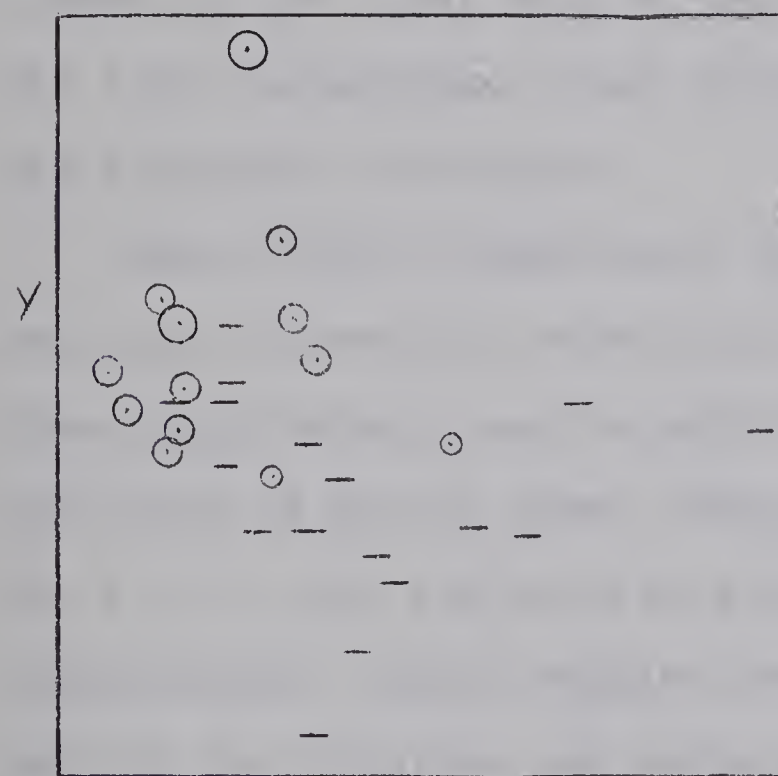
SELAGINELLA Densa



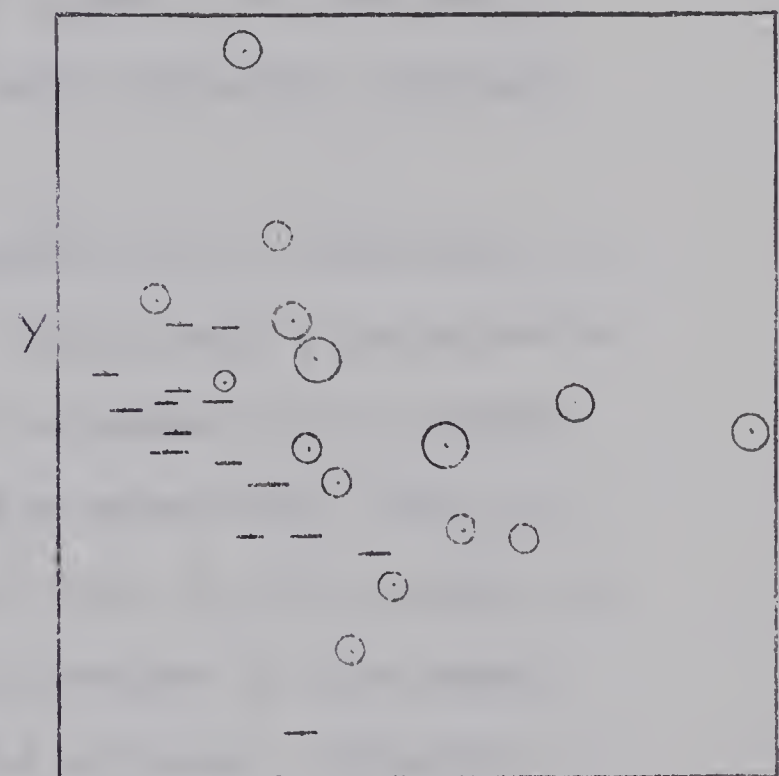
TORTULA RURALIS



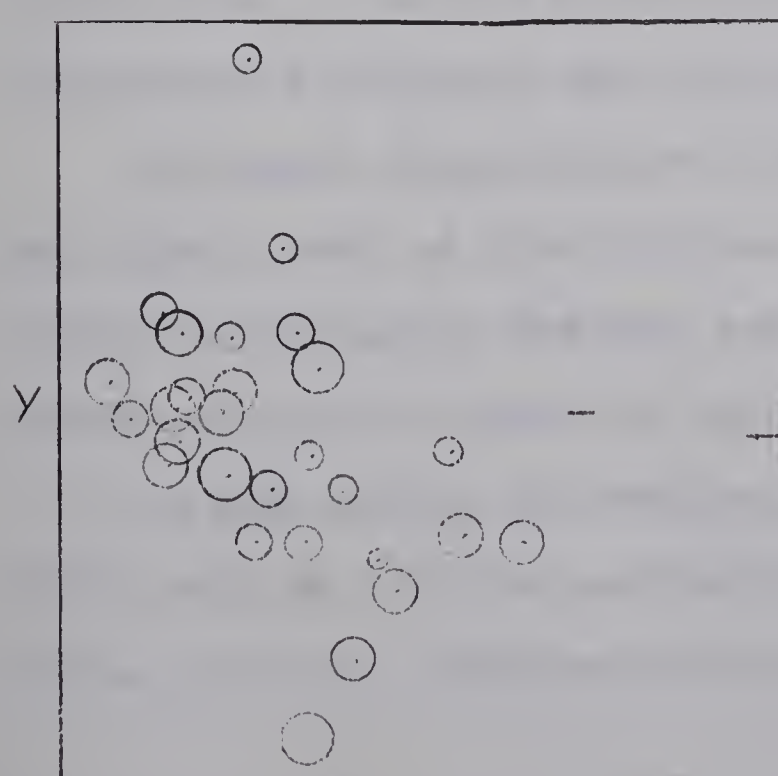
CORNICULARIA ACULEATA



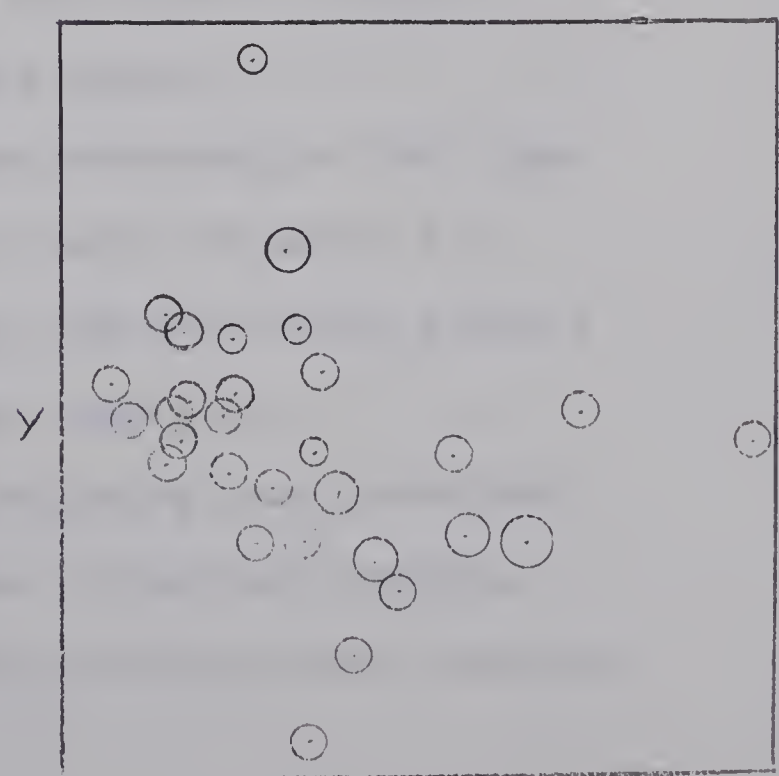
LOMATIUM MACROCARPUM



AGROPYRON DASYSTACHYUM



LUPINUS SERICEUS



GALIUM BOREALE

field, *i.e.*, the more mesic prairie stands.

The following species are at a maximum in the bottom centre of the XY plane: *Agropyron trachycaulum* var. *unilaterale*, *Bromus pumpellianus*, *Phleum pratense*; *Aster laevis* var. *geyeri*, *Fragaria virginiana* var. *glauca*, *Geranium viscosissimum* and *Vicia americana*.

The following species are most abundant in and therefore Differential to the *Poa pratensis*-*Smilacina* Meadow stands on the right side of the XY plane: *Poa pratensis* and *Stipa columbiana*; *Geum triflorum*, *Smilacina stellata* and *Taraxacum officinale*.

Many of the "understory" species, *e.g.*, *Koeleria cristata*, *Antennaria umbrinella*, *Phlox hoodii*, *Selaginella densa* and *Tortula ruralis* are most abundant in the upper left part of the XY plane, where the more xeric (Nos. 7, 62, 63, 67, 68) and heavily grazed (Nos. 5, 19) stands are concentrated. Other species most abundant in the upper left of the XY plane are *Astragalus striatus*, *Erigeron caespitosus*, *Lomatium macrocarpum* and *Senecio canus*; *Cornicularia aculeata* and *Peltigera canina*.

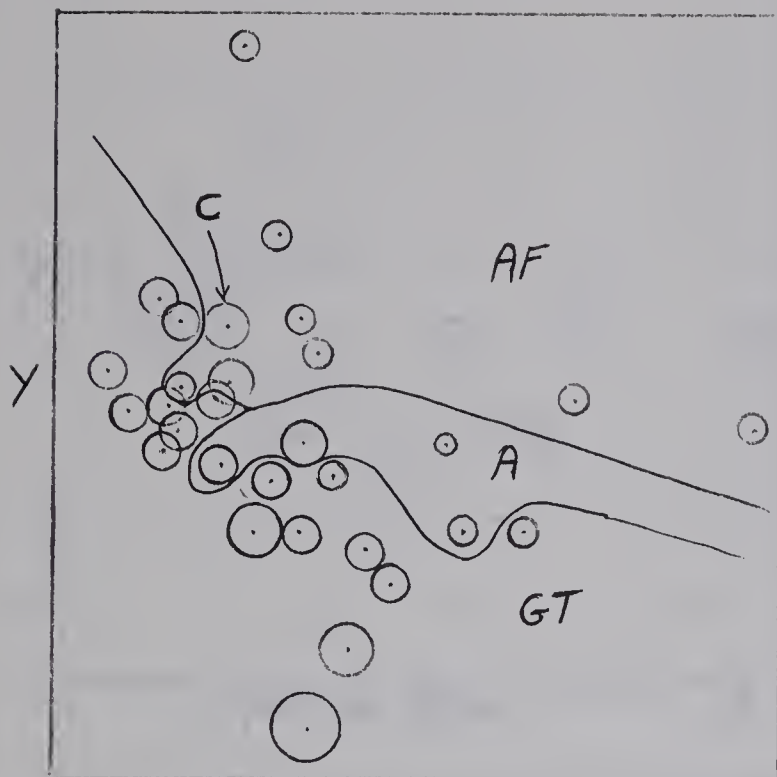
Agropyron dasystachyum is most abundant in the upper and right sides of the XY plane in both the mesic *Poa pratensis*-*Smilacina* Meadows and in the more xeric prairie stands, a pattern shown by no other species.

A large number of species, including very prominent forbs such as *Achillea millefolium*, *Cerastium arvense*, *Galium boreale*, *Gaillardia aristata*, *Lithospermum ruderales*,

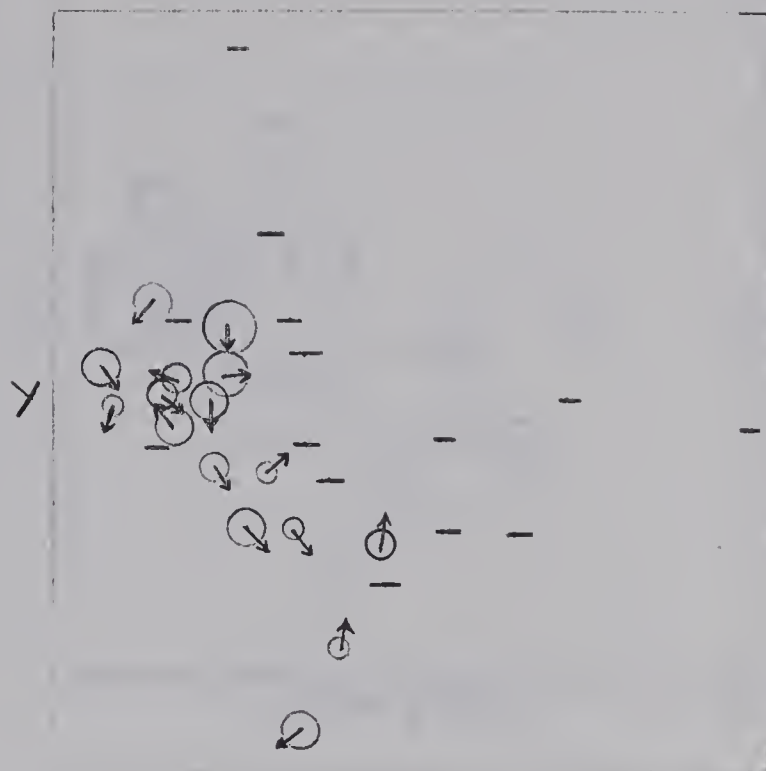
Figure 23. The distribution patterns of 14 environmental variables on the XY plane of the 30-stand *Festuca-Danthonia* Prairie ordination.

- A. Elevation and parent material: progressively larger circles represent classes of 4,000-4,195, 4,200-4,395, 4,400-4,595, 4,600-4,795, 4,800-4,995 and 5,000-5,200 ft; AF = alluvial fans, A = alluvium, GT = glacial till, C = colluvium.
- B. Slope angle and aspect: progressively larger circles represent slope angle classes of 1-2, 3-4, 5-6, 7-8 and more than 8 degrees; no slope angle represented by a dash; slope aspect indicated by the arrow pointing downslope.
- C. Sand/Clay ratio: progressively larger circles represent classes of 25.0 and over, 20.0-24.9, 15.0-19.9, 10.0-14.9, 5.0-9.9 and less than 5.0.
- D. Sand: progressively larger circles represent classes of 80-100, 70-80, 60-70, 50-60, 40-50, and less than 40%.
- E. Silt: progressively larger circles represent classes of 0-10, 10-20, 20-30, 30-40, and more than 40%.
- F. Clay: progressively larger circles represent classes of 0-5, 5-10, 10-15, 15-20, 20-25, and more than 25%.
- G. pH at 8 cm: progressively larger circles represent classes of less than 6.0, 6.0-6.4, 6.5-6.9, 7.0-7.4, 7.5-7.9 and more than 7.9.
- H. pH at 60 cm: progressively larger circles represent the same values as in "G".

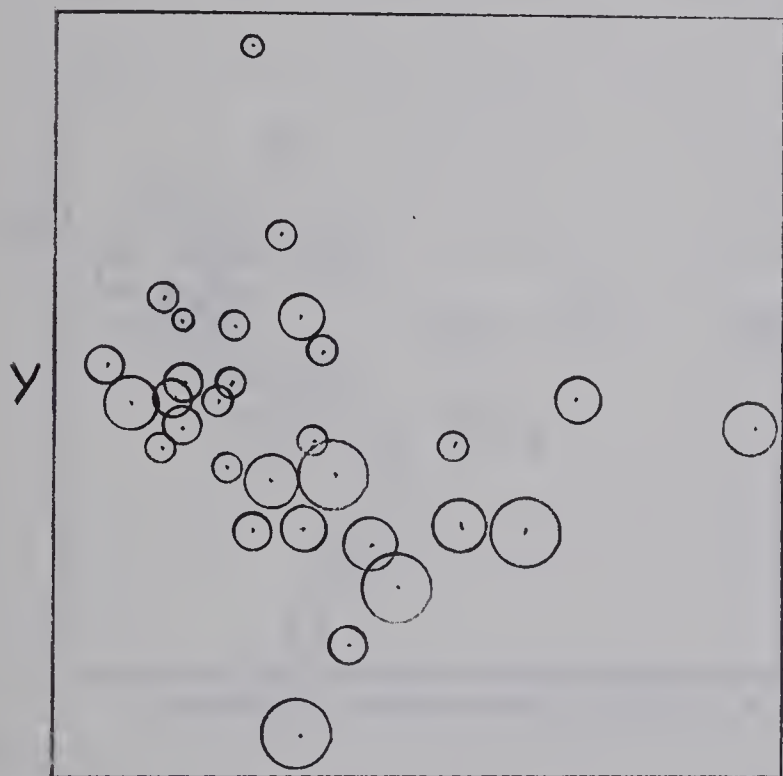
- I. Available phosphorus at 8 cm: progressively larger circles represent classes of 0-2, $2\frac{1}{2}$ - $4\frac{1}{2}$, 5-7, $7\frac{1}{2}$ - $9\frac{1}{2}$, and 10 ppm and over.
- J. Field capacity, weighted mean to 90cm: progressively larger circles represent classes of 4.0-9.9, 10.0-14.9, 15.0-19.9, 20.0-24.9, and 25-29.9%.
- K. Permanent wilting point, weighted mean to 90 cm: progressively larger circles represent classes of 0-3.9, 4.0-7.9, 8.0-11.9, 12.0-15.9, and 16.0-19.9%.
- L. Available water, weighted mean to 90 cm: progressively larger circles represent the same values as in "K".



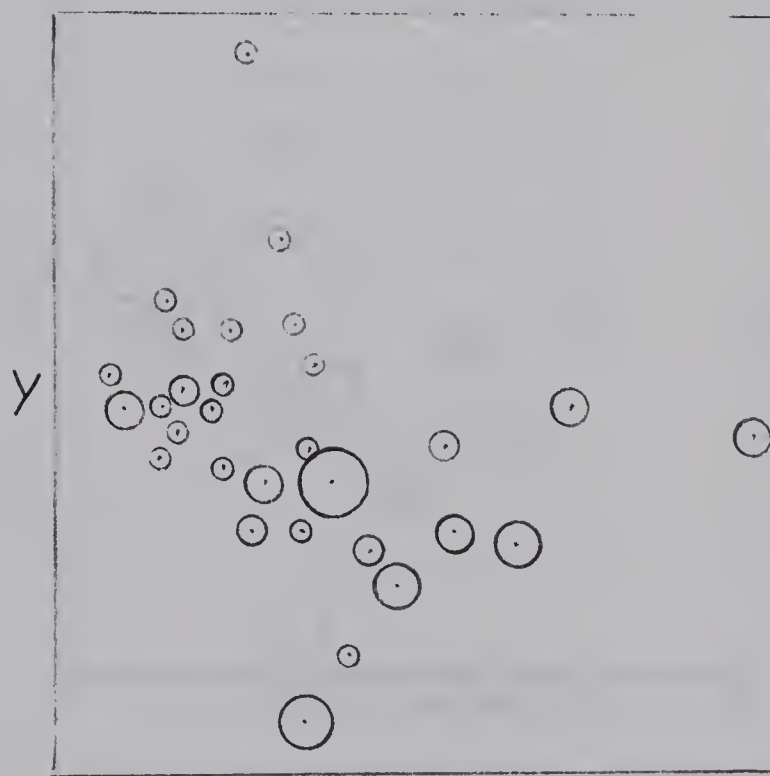
ELEVATION AND PARENT MATERIAL X



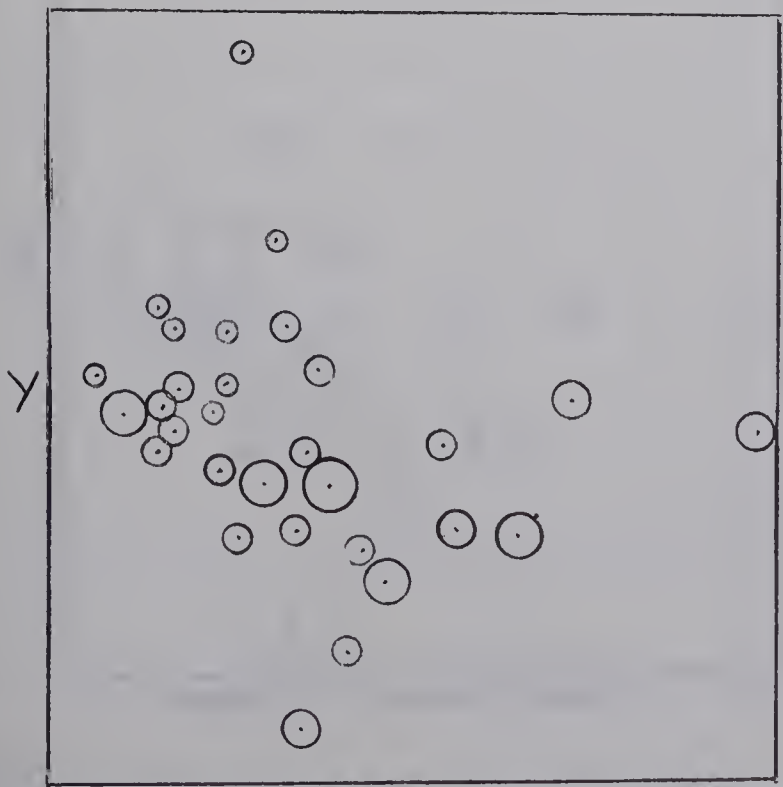
SLOPE ANGLE AND ASPECT X



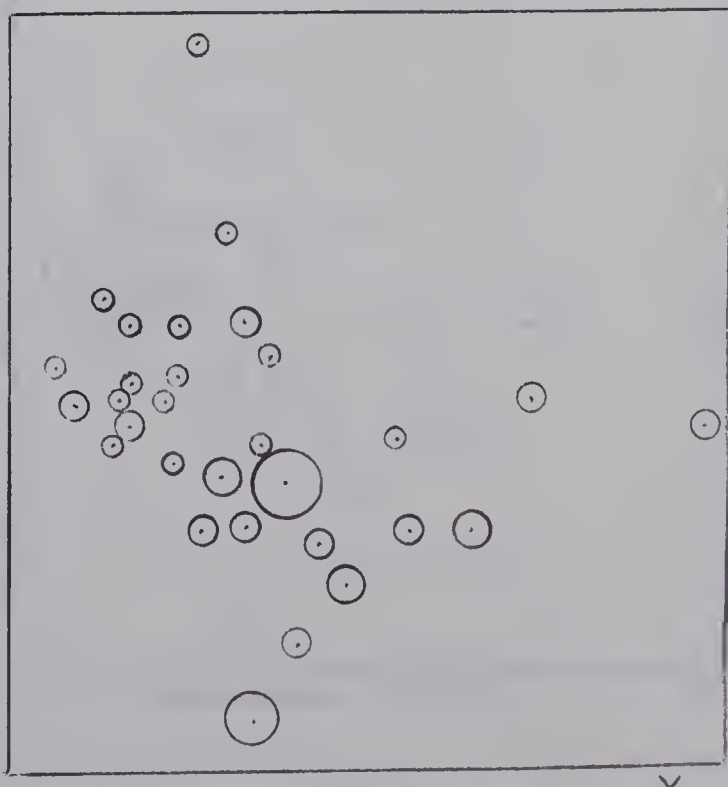
SAND/CLAY RATIO X



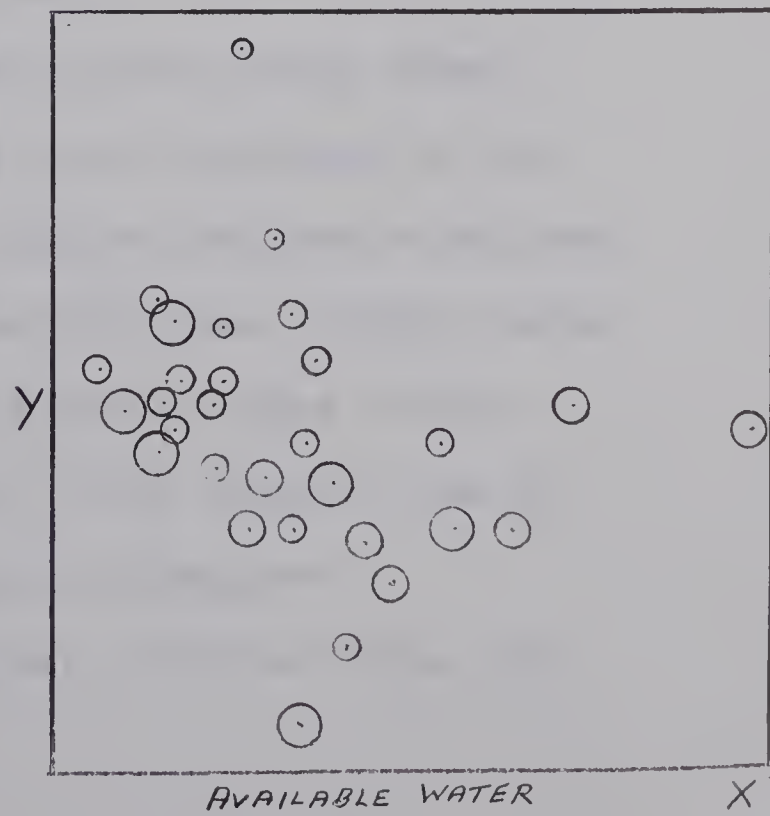
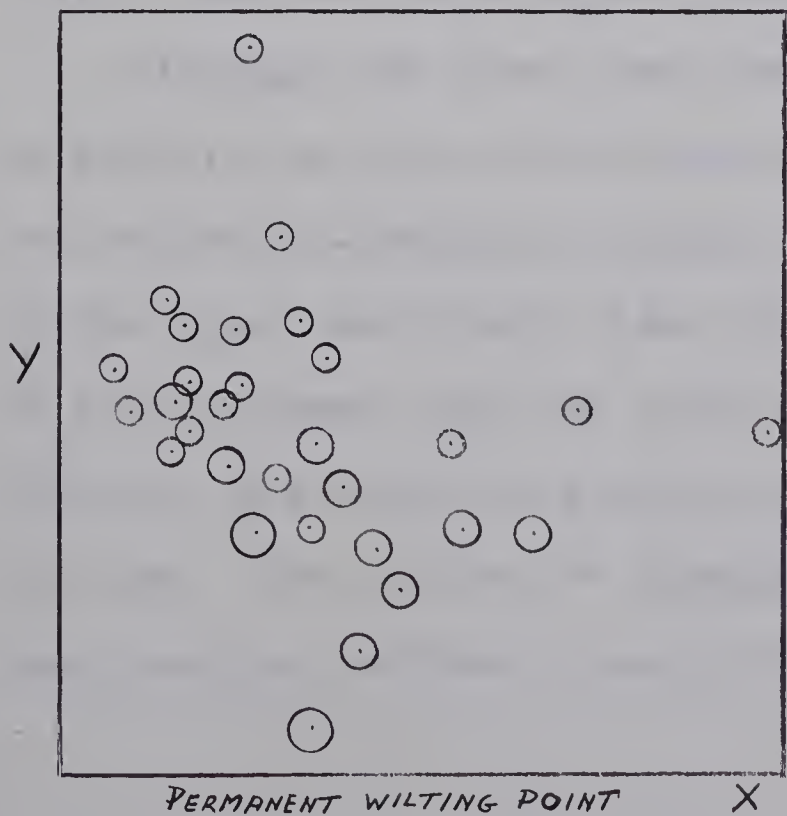
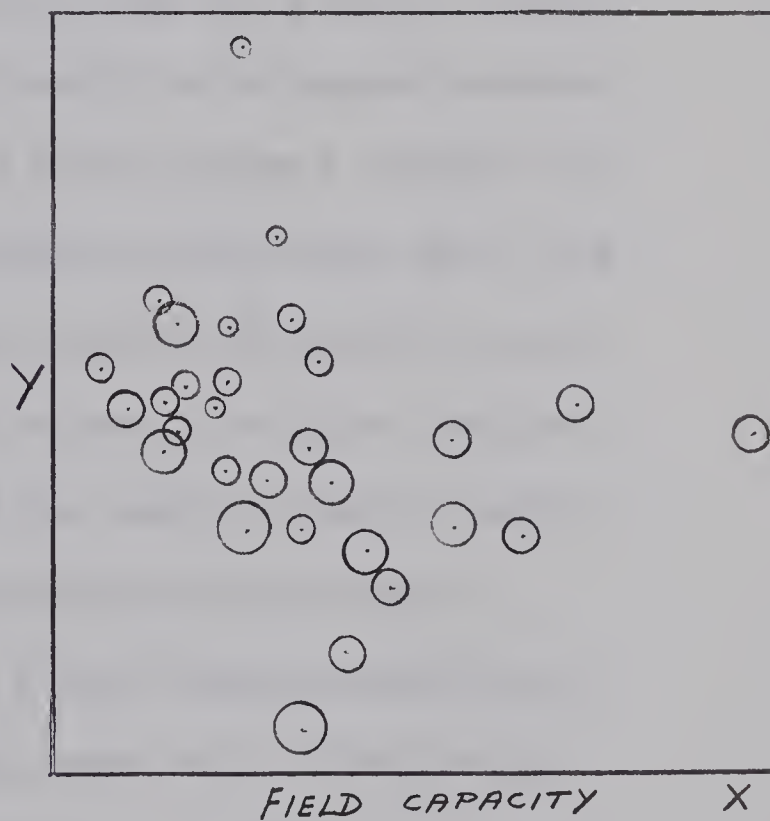
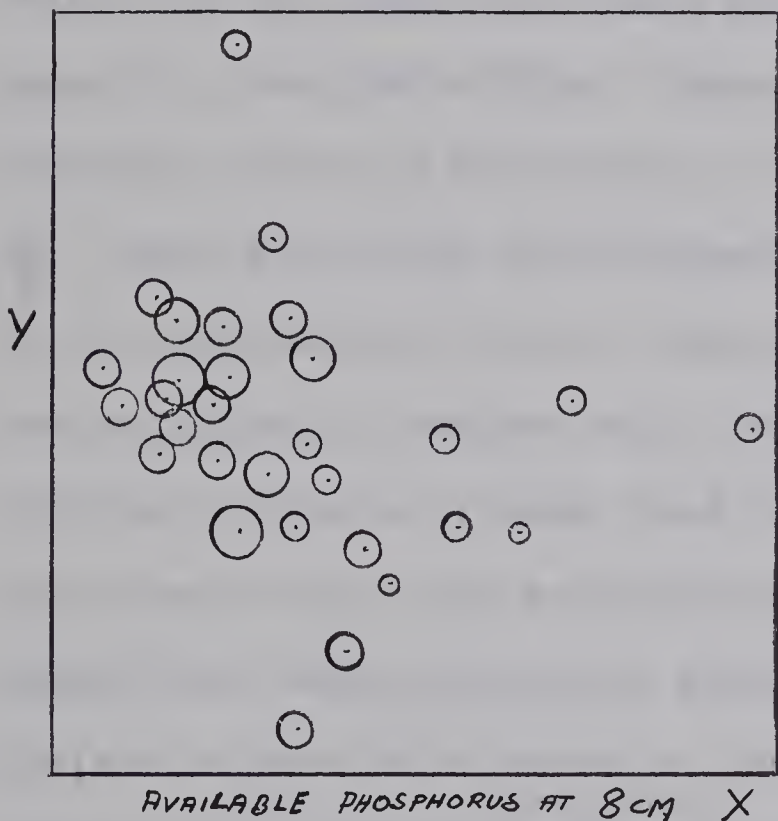
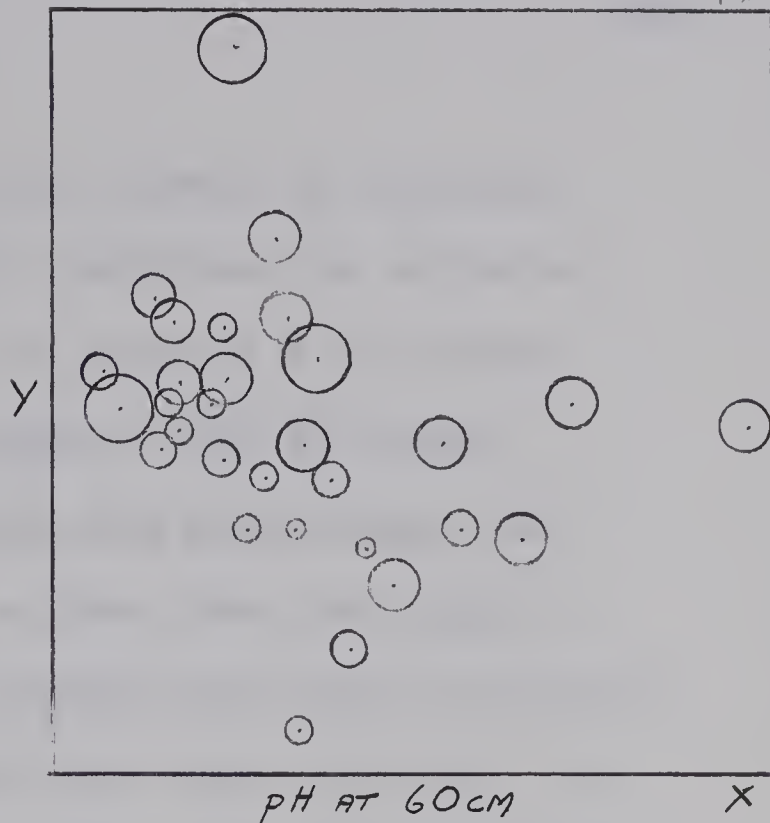
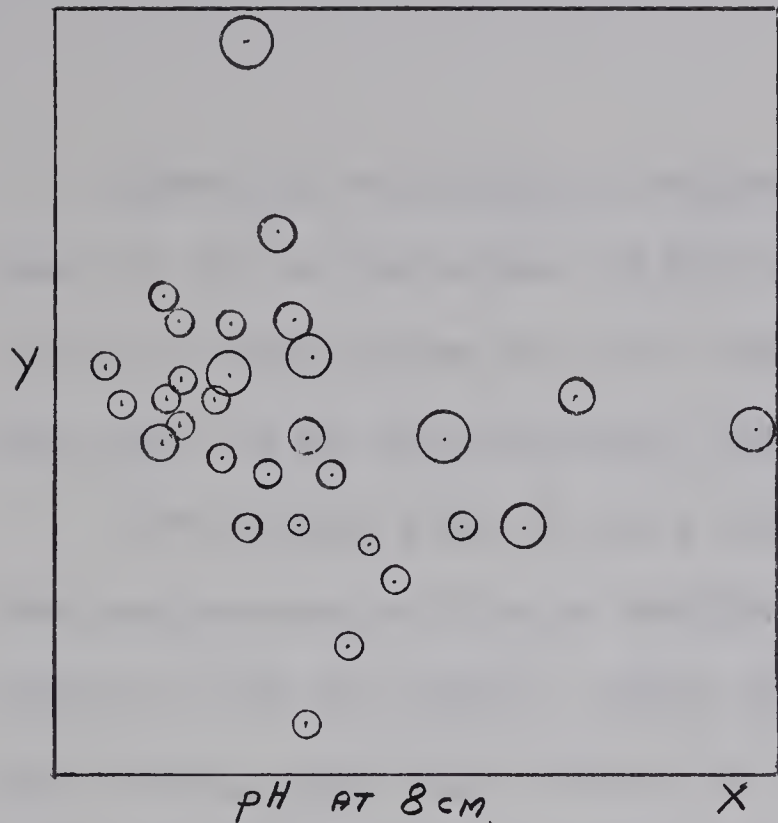
SAND X



SILT X



CLAY X



There is a distinct tendency for stands on alluvial fans to be in the upper right part, for those on alluvium to be in the centre and for those on glacial till parent material to be in the lower left part of the XY plane.

Percentage sand is at a minimum and percentage clay and percentage silt at a maximum in the lower and right parts of the XY plane. Thus, the sand/clay ratio is clearly patterned, with high values in the lower and right and low values in the upper and left parts of the XY plane. Field Capacity, Available Water Capacity and, to a lesser extent, Permanent Wilting Percentage, also have maximal values in the lower and right and minimal values in the top and left of the ordination field. Thus, the soils of the *Poa pratensis*-*Smilacina* Meadows and the more mesic of the *Festuca*-*Danthonia* Prairie stands tend to have sandy-loam or sandy clay-loam soils with relatively high Available Water Capacities, while the more xeric of the *Festuca*-*Danthonia* Prairie stands have sands or loamy-sand soils with relatively low Available Water Capacities.

Although the free lime content of the soils shows no pattern at 8 cm, free lime at 60 cm is maximal in the *Poa pratensis*-*Smilacina* stands. Soil pH reaches a maximum in the upper and right sides of the XY plane. There seems to be a tendency for the soils on alluvial fans to be alkaline and those on glacial tills to be acid in the Ah horizon. The pattern of abundance of *Agropyron dasystachyum* conforms closely to that of pH at 8 cm, and

it seems that this species is to be found principally on and is an indicator of alkaline and alluvial soils in Waterton Lakes Park.

All the higher values of available phosphorus at 8 cm are in the left centre of the XY plane. Hence, the *Poa pratensis*-*Smilacina* Meadows and many of the more mesic of the *Festuca*-*Danthonia* Prairie stands have low values for this nutrient.

Available nitrogen and potassium at 8 cm, percentage gravel, grazing activity and soil water-holding attributes show no clear trends.

To sum up, the distribution of stand on the XY ordination field can be interpreted as following two major environmental trends (Fig. 21).

1. A trend from flat, alluvial areas at lower elevations and soils with alkaline Ah horizons (top and right of the XY plane) to glacial till areas, often on slopes, and soils with acid Ah horizons (bottom and left). This roughly corresponds to a trend from moist-mesophytic *Poa*-*pratensis* Meadows and xerophytic *Festuca*-*Danthonia* Prairie to mesophytic *Festuca*-*Danthonia* Prairie.

2. A trend from high to low sand/clay ratios and a corresponding trend from low to high Available Water Capacity, from top left to bottom right of the XY plane.

8. Effects of Grazing

The pattern of grazing in Waterton grasslands is largely a result of the movements of three herds of elk. Elk in the first two herds spend summer in the high mountains in the S-E part of the Park and over the United States border. They come down to lower elevations S of the Chief Mountain highway (Highway 6) for the winter. The larger of the two herds spends the winter in the Belly River grasslands (Stand 15), and the smaller in the Stoney (Sofa) Creek area (Stands 5 and 19), and other grasslands on the E side of the Lower Waterton Lakes (Stands 2 and 11), (Pers. comm., K. Seel, Park Naturalist). Stand 16 on Lookout Butte has been heavily grazed in the past but elk have not reached the area in recent years. This has resulted in excellent re-growth of *Festuca scabrella* bunches. However, as the feces count in No. 17 was high but nil in No.7, some of the elk must reach the Cardston road (Highway 5) but do not appear to cross it (Table 7).

The third herd of elk spends the summer in the Upper Galwey Creek - Horseshoe Basin area and spreads out at lower elevations in the winter. It is thought that they keep to the areas near the bases of Lakeview Ridge, Bellevue Hill, *etc.* (fecal group counts in No. 8 = 31, No. 20 = 28), but generally do not move out to the open areas as the fecal group counts were very low in Nos. 1, 6, 7, 12, 13 and 64-71).

TABLE 7. FECAL PELLET GROUP COUNTS IN SAMPLE AREAS OF
 1,800 ft² (167m²)

WATERTON LAKES NATIONAL PARK (1967)	Stand	Native Ungu- lates	Horses	Total
	1	2	20	22
	2	45	1	46
	3	2	0	2
	4	76 ¹	0	76
	5	150	15	165
	6	0	5	5
	7	0	2	2
	8	31	12	43
	9	0	5	5
	10	0	0	0
	11	30	0	30
	12	0	0	0
	13	9 ²	5	14
	14	6 ³	1	7
	15	14 ⁴	0	14
	16	7 ⁵	1	8
	17	40 ⁶	1	41
	18	3	0	3
	19	159	1	160
	20	35	0	35
	Mean	30	4	34

WATERTON LAKES NATIONAL PARK (1968)	58 ¹⁰	36	12	48
	59	15	12	27
	60	15	21	36
	61	6	27	33
	62	9	24	33
	63	6	15	21
	64 ¹¹	12	6	18
	65	0	12	12
	66	0	2	2
	67	2	2	4
	68	2	0	2
	69	2	2	4
	70	0	3	3
	71	0	0	0
	Mean	7	10	17

Footnotes:

Most of the native ungulates are elk, except:

¹ - all big-horn sheep

² - includes about 7 mule deer

³ - includes about 4 mule deer

⁴ - includes about 12 mule deer

⁵ - includes about 5 mule deer

⁶ - includes about 21 mule deer

¹⁰ - includes about 18 deer

¹¹ - includes about 10 deer

TABLE 7. Cont'd.

146.

	<u>Stand</u>	<u>Native Ungu- lates</u>	<u>Horses</u>	<u>Total</u>
BANFF NATIONAL PARK (1967)				
	21	60	20	80
	22	0	0	0
	23	0	1	1
	24	20	0	20
	25	10	5	15
	26	10 ⁷	1	11
	27	18	0	18
	28	26	0	26
	29	61	0	61
	30	18	38	56
	31	76	40	116
	32	18	0	18
	33	0	17	17
	34	9 ⁸	0	9
	35	87	0	87
	Mean	28	8	36
JASPER NATIONAL PARK (1967)				
	36	100	0	100
	37	107	0	107
	38	97	2	99
	39	71	5	76
	40	26	3	29
	41	55	4	59
	42	72	6	78
	43	50	2	52
	44	41	2	43
	45	87	9	96
	46	18	4	22
	47	153	5	158
	48	99 ⁹	9	108
	49	75	2	77
	50	4	10	14
	51	61	1	62
	Mean	70	4	74
JASPER NATIONAL PARK (1968)				
	52	30	0	30
	53	22	2	24
	54	39	3	42
	55	33	0	33
	56	45	3	48
	57	51	12	63
	Mean	37	3	40

Footnotes: Most of the native ungulates are elk, except:

⁷ - Includes 5 mule deer and 1 moose.⁸ - Includes 3 mule deer and 1 moose.⁹ - Includes about 10 mule deer and 25 bighorn sheep.

The *Festuca-Danthonia* Prairie on the S-facing slopes of certain side valleys, notably Blakiston Brook, is frequented by bighorn sheep, *e.g.*, stand 4.

Other native ungulates were relatively unimportant. Mule deer and white-tailed deer were common in the eastern areas but of browsing habit and therefore of little consequence in the open grassland areas.

The herd of about 100 outfitters' horses grazing on the Badlands seemed to have had an adverse effect on the prairie vegetation there. Introduced species such as *Taraxacum officinale* and *Poa pratensis* have increased at the expense of the Dominant bunch grasses. Fairly high feces counts for horses were recorded from stands 1, 8 and 65 on the Badlands, as well as from areas frequented by riders (Nos. 5, 58, 62, 63) and from areas where wardens' horses have recently been pastured (Nos. 59, 61).

The long-term effects of grazing on the vegetation and soils of grasslands can best be studied by setting up exclosures. Exclosures have been set up in grasslands by biologists of the Canadian Wildlife Service, three plots being in Jasper National Park, one in Banff National Park, and three in the *Festuca-Danthonia* Prairie of Waterton Lakes National Park. The three 35 x 30 ft (11 x 9m) exclosures in the latter park were set up in 1956 in the Badlands, Lower Stoney Creek and Lookout Butte areas and are close to stands 8, 5 and 16 respectively. These three exclosures were sampled intensively during July, 1968 by

Dr. D. Flook of the Canadian Wildlife Service, in conjunction with the author (Flook and Stringer, manuscript in preparation).

The following vegetational attributes and edaphic factors were sampled inside and outside the exclosures and the differences in values tested for significance at the 5% level by Student t-tests: percentage vegetative cover by means of point quadrats, standing crop, pellet group counts, soil temperature at 15 cm, Field Capacity, Permanent Wilting Percentage, organic and inorganic carbon and moisture content of the soil at 2-5 cm and 15-20 cm depth. Full details may be found in the Flook and Stringer manuscript but the relevant conclusions are summarised as follows.

The Badlands exclosure plot is on an alluvial fan on the E-facing lower slopes of Belleview Hill. This area is often lightly grazed by elk during the winter and by horses during the summer.

The only species with significantly greater cover inside the plot was *Festuca scabrella* (Table 8); the cover of litter was also significantly higher inside. *Tortula ruralis* had a significantly higher cover outside. *Astragalus striatus* was more abundant inside and *Koeleria cristata* was more abundant outside the exclosure but in neither species were the differences significant at the 5% probability level. None of the other locally Dominant species showed any marked differences and the total cover inside was not significantly higher than that outside the exclosure. The

TABLE 8. BADLANDS EXCLOSURE PLOT.

	Mean Inside ¹	Mean Outside ¹	t ²
Litter cover, %	81.0	63.3	3.4016**
Angiosperm cover, %	91.8	84.8	1.0091
Graminoid cover, %	52.5	43.5	1.6478
<i>Koeleria cristata</i> cover, %	0.8	3.8	2.8117*
<i>Festuca scabrella</i> cover, %	20.3	4.8	4.1242**
<i>Astragalus striatus</i> cover, %	8.5	1.5	2.3726*
<i>Tortula ruralis</i> cover, %	0.8	15.3	3.5114**
Angiosperm standing crop (kg/ha)	2395	2484	0.1256
Graminoid standing crop (kg/ha)	1546	1089	1.5167
<i>Festuca scabrella</i> standing crop (kg/ha)	817	96	3.2192**
Soil temperature at 15 cm, °F	58.5	60.0	1.9641
Soil moisture at 2-5cm, %	21.4	20.1	0.4764
Soil moisture at 15-20 cm, %	8.9	7.5	1.8607
Organic carbon at 2-5 cm, %	6.6	5.6	1.4665
Organic carbon at 15-20 cm, %	3.1	2.7	1.0560

FOOTNOTES: ¹ The mean values of notable vegetational and edaphic variables inside and outside the enclosure.

² Student "t-tests"; 5% level of significance (t=3.182, 3 degrees of freedom) indicated as **, 10% level of significance (t=2.353, 3 degrees of freedom) indicated as *.

standing crop inside the enclosure was, in kg/ha: graminoids, 1,546, and forbs, 849, to give a total of 2,395 kg/ha. Again, only *Festuca scabrella* had significantly more standing crop inside the enclosure.

No soil characteristics showed any significant differences at the 5% probability level. However, outside the enclosure, mean soil temperature at 15 cm was $1\frac{1}{2}$ degrees higher and mean soil moisture lower, both at 2-5 cm and at 15-20 cm. Also, the organic carbon content of the soil was about 2% higher inside the enclosure at both depths.

Thus, it seems that the major effect of grazing has been to reduce the abundance of *Festuca scabrella* which seems to have been replaced in part by *Tortula ruralis* and *Koeleria cristata*. The increase of ground cover and litter inside the enclosure has led to slight but statistically insignificant increases in soil moisture and organic carbon content and lower soil temperatures. These changes can be verified only by more intensive sampling.

The Stoney Creek enclosure plot is on very gravelly alluvial fan deposits in an area heavily grazed by elk during the winter and early spring. Pellet group counts in an area of 1,000 ft² (292.8 m²) outside the enclosure were: elk 22, deer 1, and horse 1.

Litter was significantly more abundant inside the enclosure (Table 9), while terricolous lichens and *Koeleria cristata* were significantly more abundant outside. A number of species, including *Festuca idahoensis*, *F. scabrella*

TABLE 9. STONEY CREEK EXCLOSURE PLOT.

	Mean Inside ¹	Mean Outside ¹	t ²
Litter cover, %	89.0	29.8	12.0370**
Angiosperm cover, %	63.0	50.8	1.5613
Graminoid cover, %	41.0	32.8	1.1984
<i>Agropyron dasystachyum</i> cover, %	3.0	10.0	2.6148*
<i>Festuca idahoensis</i> cover, %	9.5	3.0	2.0273
<i>Festuca scabrella</i> cover, %	16.0	1.0	2.0195
<i>Koeleria cristata</i> cover, %	2.8	9.3	3.7791**
<i>Erigeron caespitosus</i> cover, %	0.0	3.0	---
<i>Monarda fistulosa</i> cover, %	8.8	1.5	2.8483*
Terricolous lichens cover, %	0.0	6.8	---
Angiosperm standing crop(kg/ha)	1803	1304	2.7258*
Graminoid standing crop(kg/ha)	902	806	0.7674
<i>Festuca scabrella</i> standing crop(kg/ha)	330	58	2.9073*
<i>Koeleria cristata</i> standing crop(kg/ha)	71	149	4.7624**
<i>Galium boreale</i> standing crop (kg/ha)	323	---	---
<i>Monarda fistulosa</i> standing crop(kg/ha)	176	---	---
Soil temperature at 15 cm, °F	58.0	62.8	7.5504**
Soil moisture at 2-5 cm, %	17.2	12.1	1.3310
Soil moisture at 15-20 cm, %	12.8	8.4	2.3810*
Organic carbon at 2-5 cm, %	3.0	2.1	0.8406
Organic carbon at 15-20 cm, %	1.3	2.0	1.4423

Footnotes: ¹ see Table 8, p.149.² see Table 8, p.149.

and *Monarda fistulosa* var. *menthaefolia*, had higher cover inside, but the differences were not statistically significant because of wide sampling variation. *Agropyron dasystachyum* had higher but statistically insignificant cover outside the plot. *Erigeron caespitosus* was very prominent outside but absent from inside the exclosure.

The total standing crop inside the exclosure was 1,803 kg/ha, *i.e.*, about 901.5 kg/ha each of graminoids and forbs. *Galium boreale* and *Monarda fistulosa* var. *menthaefolia* had respectively 323 and 176 kg/ha of standing crop inside the exclosure but none outside, at least in the plots clipped. The standing crop of *Koeleria cristata* was significantly higher outside; those of *Festuca scabrella* and of total vascular plants were higher inside but the differences were not quite significant at the 5% level.

The soil profile of this Orthic Regosol had a shallower Ah horizon (2 cm inside; <1 cm outside) and more gravel near the surface outside the exclosure, indicating erosion. Although organic carbon percentage at 2-5 cm and mean soil moisture at 2-5 cm and 15-20 cm were higher inside the exclosure, the differences were not significant at the 5% probability level. However, mean soil temperature at 15 cm was significantly lower inside the exclosure.

Heavy grazing has inhibited the build-up of humus, has increased soil aridity and led to soil erosion and to the partial replacement of species, such as *Festuca* spp., *Galium boreale* and *Monarda fistulosa* by *Koeleria cristata*,

Erigeron caespitosus and terricolous lichens such as *Cornicularia aculeata* and *Cladonia* spp..

The Lookout Butte exclosure plot is on glacial till in an area which has been almost free of grazing for several years.

At the 5% probability level, the only significant difference in cover was the greater abundance of *Arctostaphylos uva-ursi* outside the plot (Table 10). There were no significant differences in standing crops of total vascular plants or of any of the following locally Dominant species: *Calamagrostis rubescens*, *Festuca scabrella*, *Carex* spp., *Anemone patens* var. *wolfgangiana*, *Aster laevis* var. *geyeri*, *Hedysarum sulphurescens*, *Rosa* spp., *Solidago missouriensis*, *Zygadenus elegans*.

The total standing crop inside the exclosure was 4,306 kg/ha, i.e., 646 kg/ha of graminoids and 3,660 kg/ha of forbs and dwarf shrubs; 2,967 kg/ha of the latter figure was new growth of *Arctostaphylos uva-ursa*.

The proximity of small aspens, the prominence of several shrub species and aspen suckers inside the plot, and the local abundance of *Calamagrostis rubescens* all indicate that this area is transitional between grassland and aspen woodland, and may formerly have been wooded.

The soil profile looked identical inside and outside the exclosure and there were no significant differences in any soil characteristics.

TABLE 10. LOOKOUT BUTTE EXCLOSURE PLOT.

	Mean Inside ¹	Mean Outside ¹	t ²
Litter cover, %	90.3	91.5	0.4293
Angiosperm cover, %	105.00	122.0	1.8967
Graminoid cover, %	29.3	18.8	2.8801*
<i>Arctostaphylos uva-ursi</i> cover, %	40.8	60.3	3.9164**
Angiosperm standing crop (kg/ha)	4306	5199	2.0801
Graminoid standing crop (kg/ha)	646	500	1.2489
Soil temperature at 15 cm, °F	53.0	52.8	0.2641
Soil moisture at 2-5 cm, %	31.3	32.4	0.1719
Soil moisture at 15-20 cm, %	13.7	17.0	2.3917*
Organic carbon at 2-5 cm, %	7.5	6.0	0.7469
Organic carbon at 15-20 cm, %	1.7	1.4	1.2319

Footnotes: ¹ see Table 8, p.149.

² see Table 8, p.149.

9. Intensive Study of the Badlands Area

The Badlands has large expanses of undisturbed *Festuca-Danthonia* Prairie and is therefore very suitable for a study of the interrelations of microenvironments and vegetation patterns in this grassland type. The terrain is gently undulating and the parent material a coarse, gravelly glacial till.

A transect was laid along a very gentle, S-E-facing slope (stand 65), into a slight depression (stand 66), on to the flat top of a ridge which was probably a drumlin (stand 69), and down a gentle, N-facing slope (stand 70) into a gully (stand 71). Stand 64 was $\frac{1}{4}$ mile to the W on a gentle, S-facing slope with similar parent material (Fig. 25, p. 156). A topographic profile along the transect is shown in Fig. 24, p. 156.

The data from these eight stands were used to investigate the effects of slope exposure and angle, local elevation and various edaphic factors on the distribution and abundance of the most prominent plant species present. The grazing factor was considered negligible as the transect area has been very little browsed or grazed by ungulates for many years. The pellet group count was very low or nil in all stands except Nos. 64 and 65 (Table 7). Native ungulates, mostly mule deer, had grazed or browsed a little in No. 64; No. 65 which was close to a riding trail had a low pellet group count for horses.

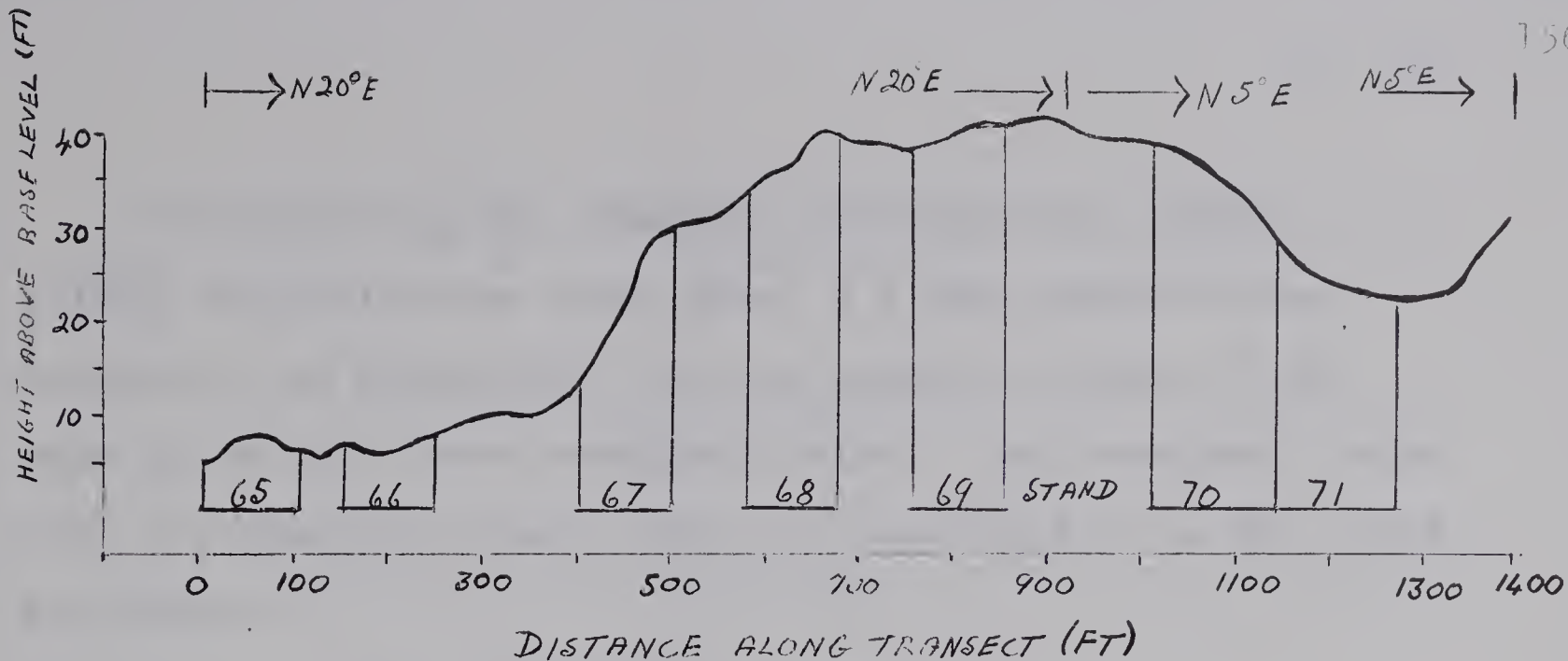


FIG. 24 TOPOGRAPHICAL PROFILE ACROSS BADLANDS INTENSIVE SITE
 SCALE. VERTICAL. 1CM $\equiv$ 10FT.
 HORIZONTAL. 1CM $\equiv$ 100FT.

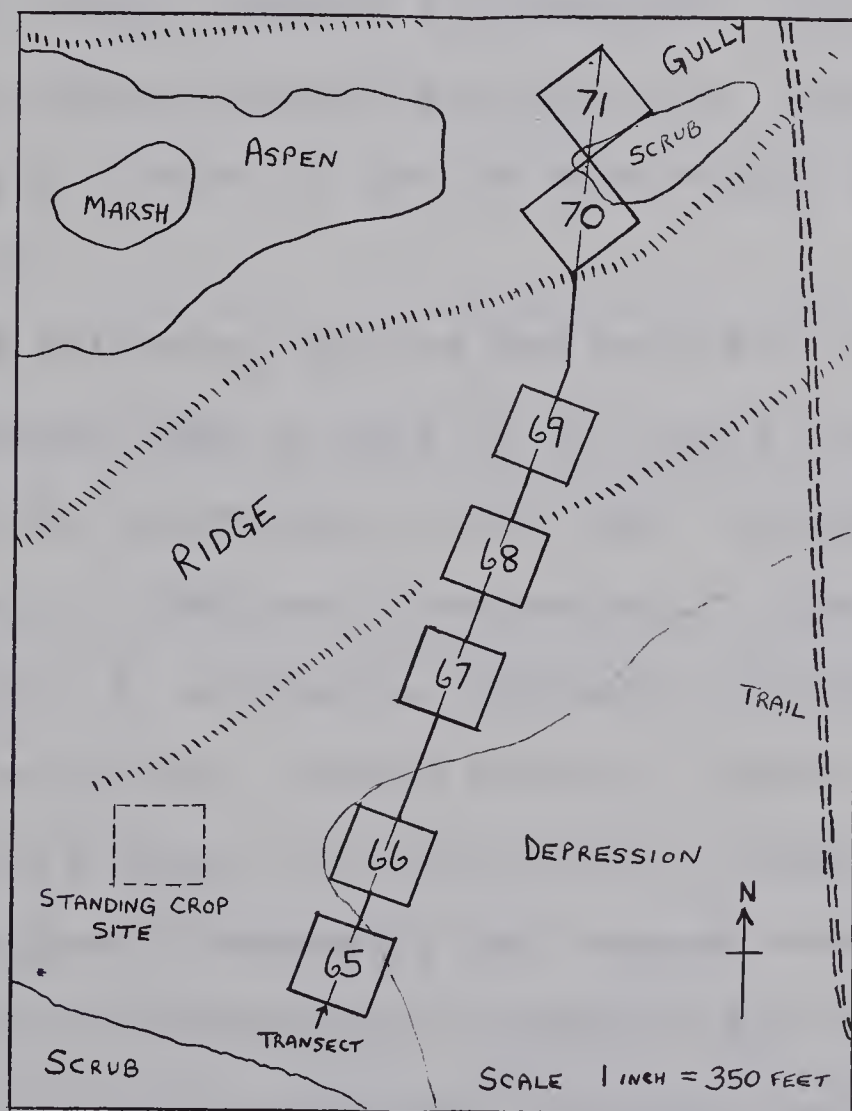


FIG. 25 BADLANDS INTENSIVE STUDY SITE, WATERTON
 LAKES NATIONAL PARK.
 SHOWING STANDS 65-71

In describing the abundance of individual species within this intensive study area, a single quantitative expression of population size was sought in place of the more subjective Cover-abundance value. The Prominence Index (PI) introduced by Beals (1960) and modified by La Roi (1964) was chosen:

$$PI = \sqrt{\text{Frequency}} \times \text{Cover}.$$

This Index was calculated for all species in each stand, from the quadrat frequency and point quadrat cover data, and the results rounded to integrals. The minimum PI value for any species present was set at 1. Species with mean PIs of 0.5 or more in one or more stands are listed in Table 11.

The following species had mean PIs of 10.0 or more, and together made up most of the total above-ground standing crop of the vegetation in the area: *Calamagrostis rubescens*, *Carex* spp.,⁹ *Danthonia intermedia*, *D. parryi*, *Festuca idahoensis*, *F. scabrella*, *Koeleria cristata*; *Anemone* spp.,¹⁰ *Cerastium arvense*, *Galium boreale*, *Lupinus sericeus*; *Selaginella densa*; *Tortula ruralis*; *Cladonia* spp..

Danthonia intermedia and *Festuca scabrella* are most prominent in depressions (stands 66 and 71) (Fig. 26), together with *Calamagrostis rubescens* and *Poa pratensis*

⁹ Includes *C. heliophila*, *C. obtusata* and *C. xerantica*; indistinguishable in vegetative state in field.

¹⁰ *A. multifida* and *A. patens* var. *wolfgangiana*; vegetatively indistinguishable.

TABLE 11. VEGETATION STRUCTURE AND POPULATION SIZES OF THE BADLANDS INTENSIVE STUDY AREA

Prominence indices (Cover x $\sqrt{\text{Frequency}}$) of all species with mean values of 0.5 or more, and Cover (%) of vegetation strata; another 8 grasses and sedges, 31 forbs, 6 bryophytes and 1 lichen were also recorded and have been listed in Appendices 4 and 5.

	Stand	64	65	66	67	68	69	70	71	Mean
Total Angiosperm Cover, %		93.4	73.0	97.5	69.4	64.2	65.6	80.6	97.0	
Shrub Cover, %		2.2	0.7	2.1	0.1	3.1	0.0	1.3	5.2	
<i>Rosa woodsii</i>		8	5	17	1	29	1	3	4	8.5
<i>Amelanchier alnifolia</i>		0	0	1	0	0	1	2	38	5.3
<i>Potentilla fruticosa</i>		3	1	1	0	0	0	0	0	0.6
Dwarf Shrub Cover, %		0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	
<i>Arctostaphylos uva-ursi</i>		0	0	0	0	0	1	0	9	1.3
Graminoid Cover, %		53.0	43.1	71.6	30.6	25.4	32.1	43.6	66.2	
<i>Festuca scabrella</i>		140	155	227	77	30	50	159	261	137.4
<i>Danthonia parryi</i>		67	35	124	99	93	164	119	16	89.6
<i>Festuca idahoensis</i>		220	138	94	53	73	52	42	11	85.4
<i>Danthonia intermedia</i>		22	34	71	3	4	6	22	68	28.8
<i>Carex</i> spp. (3) ¹		18	39	86	44	26	29	61	39	42.8
<i>Calamagrostis rubescens</i>		0	0	0	0	0	0	0	143	17.9
<i>Koeleria cristata</i>		18	8	8	16	14	7	9	3	10.4
<i>Poa pratensis</i>		0	1	15	0	0	0	0	42	7.3
<i>Stipa columbiana</i>		21	10	10	3	1	1	6	3	6.9
<i>Agropyron trachycaulum</i>										
var. <i>unilaterale</i>		1	1	12	0	1	0	1	2	2.3
<i>Helictotrichon hookeri</i>		4	1	4	1	2	4	1	0	2.1
<i>Stipa richardsonii</i>		0	0	9	1	0	0	0	4	1.8
<i>Agropyron spicatum</i>		1	1	2	2	4	1	1	0	1.5
<i>Bromus pumellianus</i>		0	1	3	0	0	1	2	3	1.3
<i>Calamagrostis montanensis</i>		0	0	0	1	1	1	1	0	0.5
Forb Cover, %		24.2	19.3	21.6	23.3	17.6	18.6	30.1	23.1	
<i>Lupinus sericeus</i>		63	87	19	84	26	26	91	1	49.6
<i>Galium boreale</i>		37	33	35	24	33	39	39	59	37.4
<i>Anemone</i> spp. ²		15	27	13	18	31	31	36	13	23.0

TABLE 11. Cont'd.

Stand	64	65	66	67	68	69	70	71	Mean
<i>Cerastium arvense</i>	25	20	9	9	16	12	20	2	14.1
<i>Achillea millefolium</i>	19	3	11	7	3	2	16	9	8.8
<i>Erigeron caespitosus</i>	1	22	1	11	4	11	19	0	8.6
<i>Agoseris glauca</i>	40	1	1	6	2	1	1	1	6.6
<i>Penstemon confertus</i>	1	1	17	2	1	1	2	27	6.5
<i>Antennaria umbrinella</i>	1	2	1	12	7	2	17	2	5.5
<i>Geranium viscosissimum</i>	0	0	13	0	0	0	0	28	5.1
<i>Aster laevis</i> var. <i>geyeri</i>	1	1	3	1	1	22	2	7	4.8
<i>Monarda fistulosa</i> var. <i>menthaefolia</i>	1	0	21	1	0	0	0	5	3.5
<i>Potentilla gracilis</i>	1	1	10	1	1	0	6	3	2.9
<i>Fragaria virginiana</i>									
var. <i>glauca</i>	0	0	3	0	0	0	0	19	2.8
<i>Campanula rotundifolia</i>	4	1	4	2	3	2	3	1	2.5
<i>Arenaria capillaris</i>	0	1	1	3	7	4	1	0	2.1
<i>Astragalus decumbens</i>									
var. <i>serotinus</i>	6	1	0	4	1	1	4	0	2.1
<i>Gaillardia aristata</i>	3	4	1	2	4	1	1	1	2.1
<i>Hedysarum sulphurescens</i>	2	2	1	1	3	6	1	0	2.0
<i>Potentilla arguta</i>	0	1	5	2	1	0	0	1	1.3
<i>Allium cernuum</i>	1	1	1	1	1	1	1	1	1.0
<i>Arabis nuttallii</i>	1	1	1	1	1	1	1	1	1.0
<i>Solidago missouriensis</i>	1	0	1	1	1	1	2	1	1.0
<i>Antennaria pulcherrima</i>	0	0	1	0	0	0	1	5	0.9
<i>Oxytropis sericea</i>									
var. <i>spicata</i>	1	1	0	1	1	3	0	0	0.9
<i>Chrysopsis villosa</i>	0	1	1	1	2	0	1	0	0.8
<i>Comandra pallida</i>	1	1	0	1	2	1	0	0	0.8
<i>Potentilla hippiana</i>	1	1	1	1	1	0	1	0	0.8
<i>Silene parryi</i>	0	1	0	1	1	2	1	0	0.8
<i>Zizia aptera</i>	0	1	0	0	0	0	1	5	0.8
<i>Androsace septentrionalis</i>	0	1	0	1	1	0	1	1	0.6
<i>Heuchera flabellifolia</i>	1	0	0	0	1	0	2	1	0.6
<i>Castilleja septentrionalis</i>	1	0	0	1	1	1	1	0	0.6

TABLE 11. Cont'd.

Stand	64	65	66	67	68	69	70	71	Mean
<i>Astragalus striatus</i>	0	1	0	1	1	0	1	0	0.5
<i>Bupleurum americanum</i>	0	0	0	1	1	1	1	0	0.5
<i>Calochortus apiculatus</i>	1	1	0	0	0	1	1	0	0.5
<i>Heuchera cylindrica</i>	0	0	1	0	0	0	1	2	0.5
<i>Lomatium macrocarpum</i>	0	0	0	1	1	1	1	0	0.5
<i>Sedum stenophyllum</i>	0	0	0	1	1	0	1	1	0.5
<i>Taraxacum officinale</i>	0	0	1	1	1	0	1	0	0.5
<i>Zygadenus elegans</i>	0	0	1	0	0	2	1	0	0.5
Pteridophyte Cover, %	14.0	9.9	2.2	15.4	18.1	14.9	5.6	0.1	
<i>Selaginella densa</i>	134	99	12	150	181	149	53	1	97.4
Bryophyte Cover, %	5.0	3.3	0.2	1.0	2.4	1.9	1.7	0.1	
<i>Tortula ruralis</i>	46	31	1	8	14	18	12	0	16.2
<i>Polytrichum juniperinum</i>	0	0	0	1	3	0	2	1	0.9
Lichen Cover, %	0.2	3.9	0.9	8.6	13.5	10.2	4.6	0.0	
<i>Cladonia</i> spp.	1	31	3	63	63	90	28	1	35.0
<i>Cornicularia aculeata</i>	0	1	1	4	34	5	5	0	6.3
<i>Peltigera canina</i>	0	1	1	5	12	1	1	0	2.6
<i>Ochrolechia upsaliensis</i>	0	1	0	3	2	1	0	0	0.9
<i>Parmelia chlorochroa</i>	0	0	1	0	4	1	0	0	0.8
<i>Physcia muscigena</i>	0	0	0	1	3	0	1	0	0.6
<i>Cetraria ericetorum</i>	0	0	0	1	1	1	1	0	0.5

Footnotes: ¹ Includes *Carex heliophila*, *C. obtusata* and *C. xerantica*.

² Includes *Anemone multifida* and *A. patens* var. *wolfgangiana*.

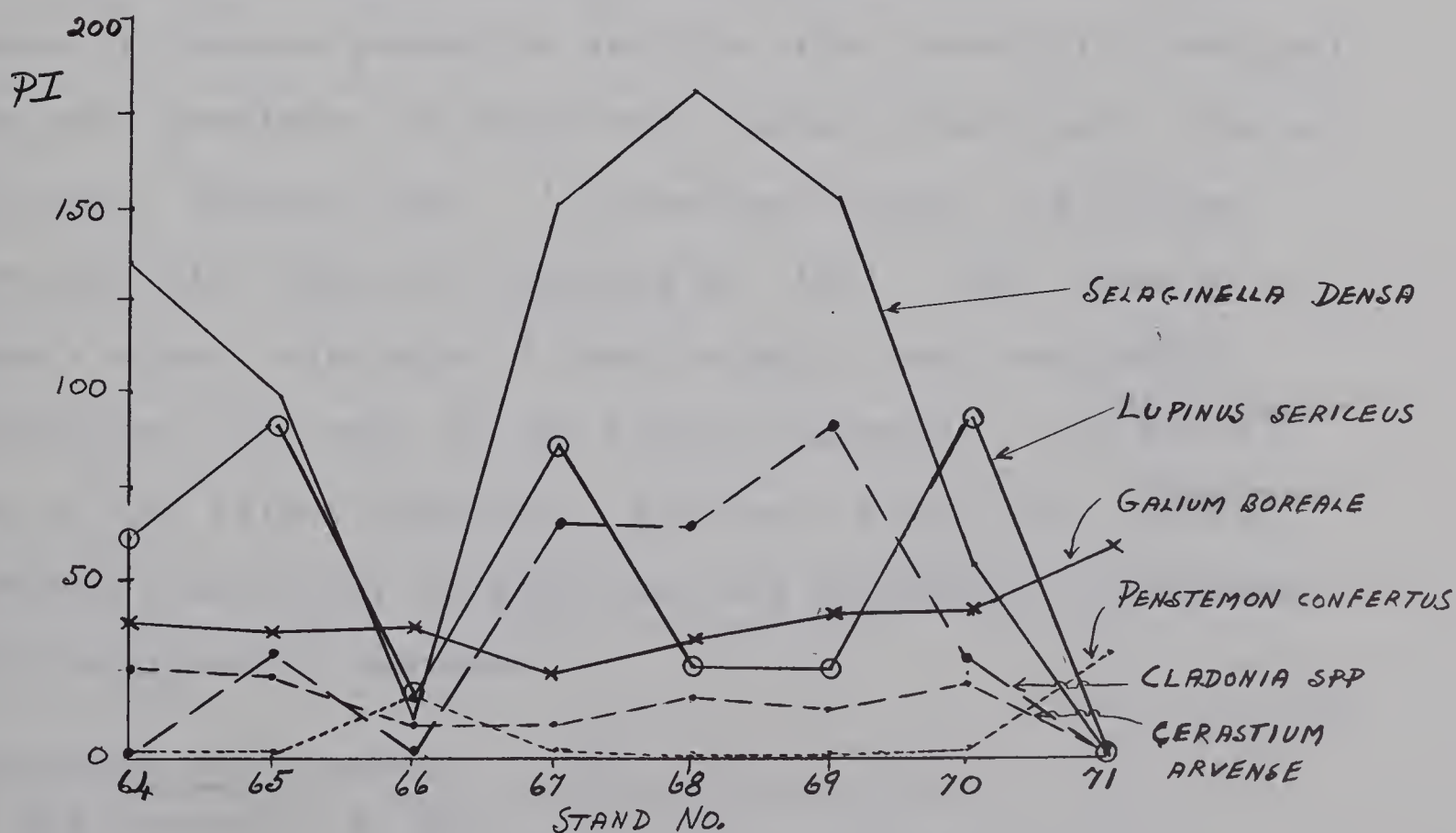
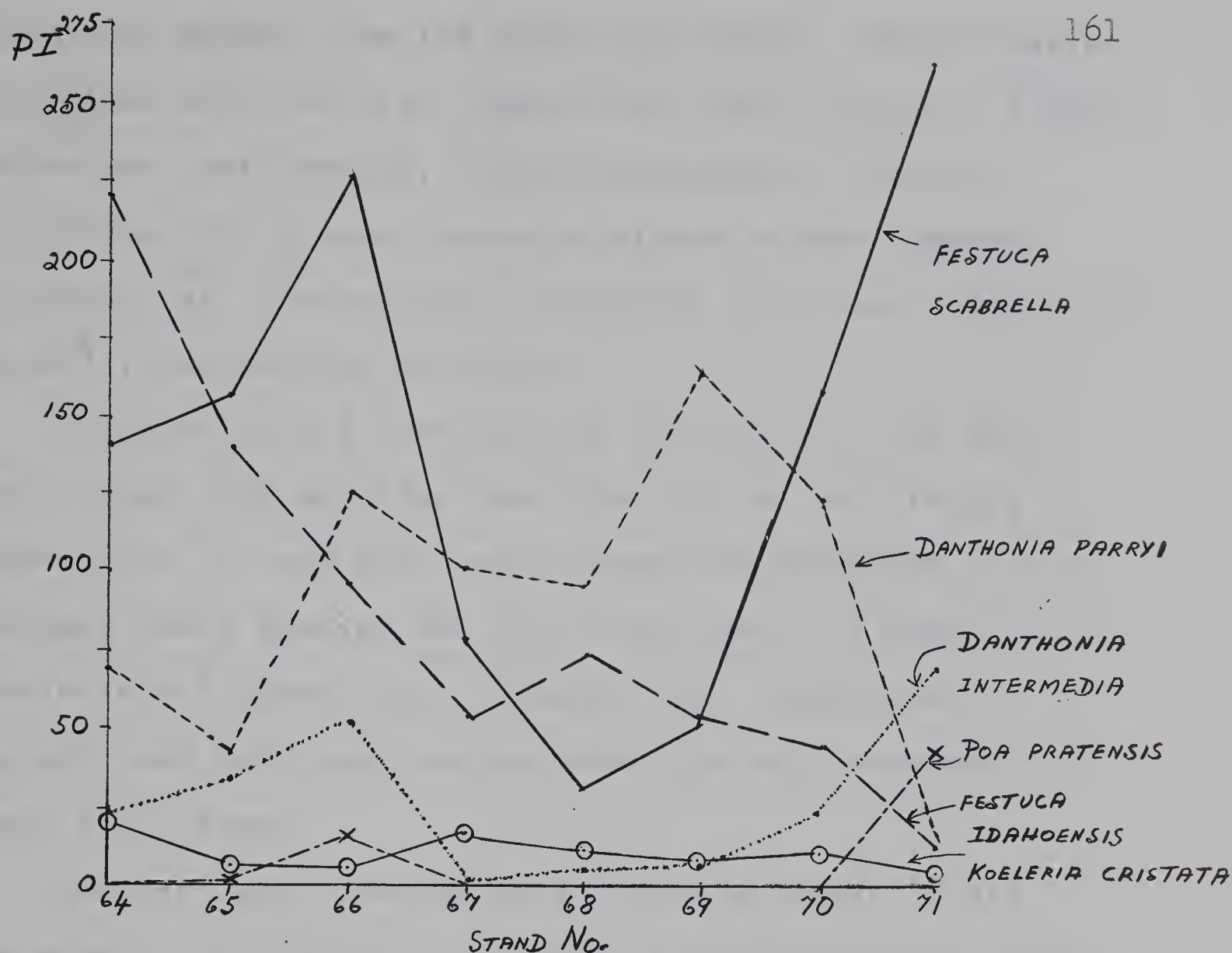


FIG. 26 PROMINENCE INDICES OF 12 SELECTED SPECIES
IN THE BADLANDS INTENSIVE STUDY SITE.

which were absent from the other six stands. Other species associated with the mesic depressions were *Agropyron trachycaulum* var. *unilaterale*, *Stipa richardsonii*, *Fragaria virginiana* var. *glauca*, *Geranium viscosissimum*, *Monarda fistulosa* var. *menthaefolia*, *Penstemon confertus*, *Potentilla gracilis*; *Amelanchier alnifolia*.

Selaginella and *Tortula* were prominent in the more xeric areas such as ridge tops (No. 69) or on S-facing slopes (Nos. 67 and 68), areas where the abundance of the Dominant bunch grasses and forbs was lower. A number of terricolous lichens, e.g., *Cladonia* spp., *Cornicularia aculeata* and *Peltigera canina* were also very prominent in these xeric areas.

However, many species were fairly abundant in all the stands and seemed to be little influenced by the abundance of *Festuca scabrella* and the other mesophytic Dominants. The most prominent of these were *Festuca idahoensis*, *Koeleria cristata*, *Anemone* spp., ¹¹ *Cerastium arvense* and *Galium boreale*, all understory species (p. 115). They seem to have a wider tolerance of local edaphic and topographic variations than most of the taller Dominants. The PIs of two of the taller Dominants, *Danthonia parryi* and *Lupinus sericeus*, were very variable and not obviously correlated with topographic features.

¹¹ See footnote, p. 157

The total flowering plant cover was higher in stands in depressions (Nos. 66 and 71) and lower in xeric stands (Nos. 67, 68 and 69) (Fig. 27).

All the soils were Orthic Black Chernozems, except that in stand 68, which was a Rego Black Chernozem. Gravel content of the mineral soil was 20-40% in the depressional areas (Nos. 66 and 71), and up to 70% in some of the higher areas (No. 68), where gravel came to within 5 cm of the surface (Fig. 27). The <2 mm fractions of the mineral horizons were all sandy-loams, loamy-sands or sands, and generally became coarser with depth. The B horizons were poorly defined and the depth of the Ah horizons therefore usually difficult to determine. This depth varied from about 25 cm in stand 66 to about 8 cm in stands 67, 68 and 69. Free lime was absent from all horizons as far as 90 cm depth, except in stand 69; this latter profile had, from 48 cm downwards, a dense, light-coloured horizon with a high lime content and a pH of 8.1. The Ah horizons of the soils were all acid with pH values ranging from 6.0 to 6.5 in the more xeric sites and from 5.5 to 6.0 in the mesic sites in depressions.

The amounts of available nitrogen, phosphorus and potassium usually decreased with depth (Appendix 9, p. 330). In the Ah horizons, available nitrogen was very low or nil. It was highest in stand 64 (6 ppm) which was sampled in June, a month earlier than the other stands. This difference suggests a progressive depletion of available nitrogen through the first part of the growing season. The ranges of

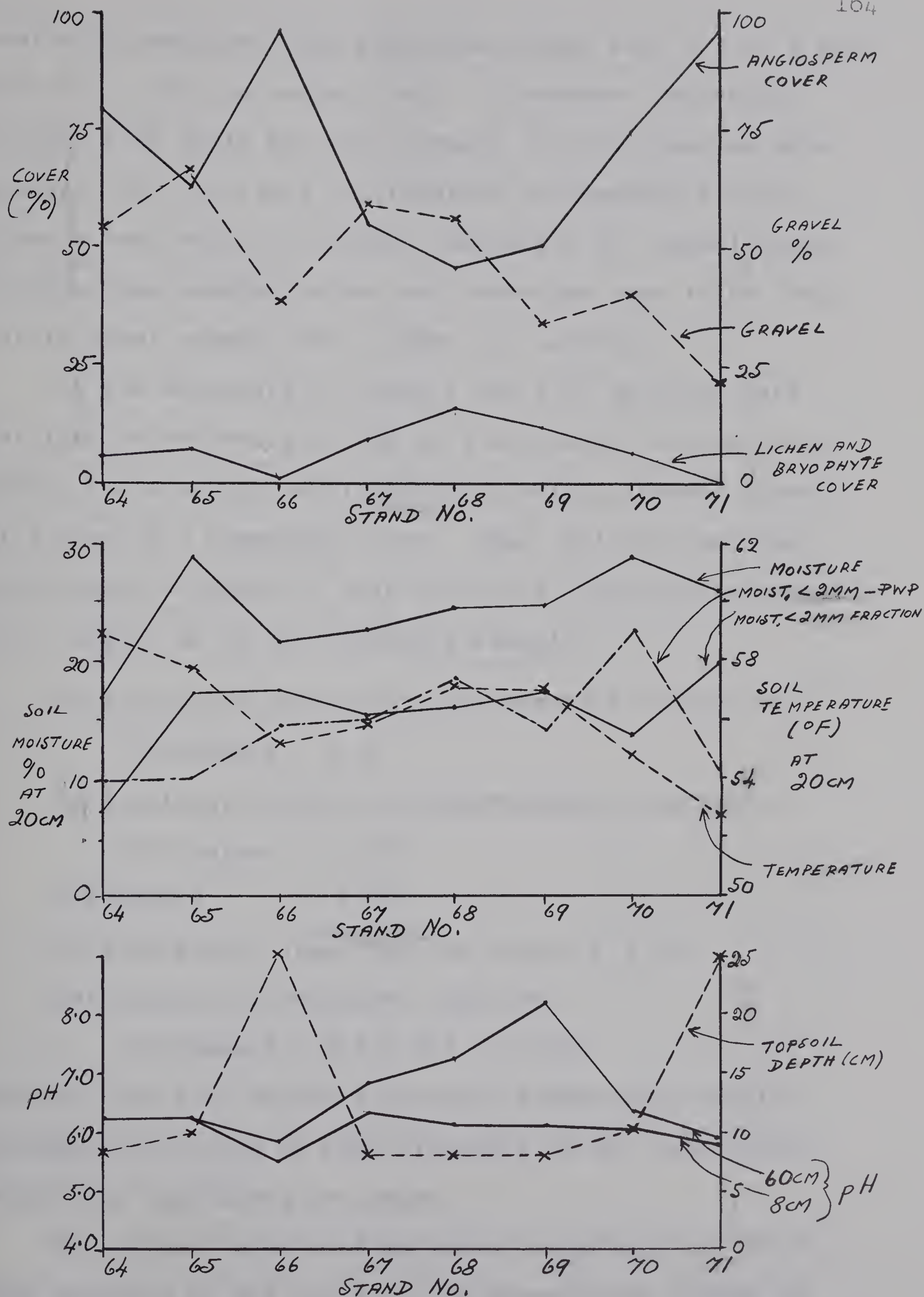


FIG. 27 VEGETATIONAL ATTRIBUTES AND ENVIRONMENTAL VARIABLES IN THE BADLANDS INTENSIVE STUDY SITE

available phosphorus and potassium values were 4.5 to 8 ppm and 170 to 258 ppm respectively. Phosphorus decreased rapidly with depth but the decrease in potassium was more gradual. On the basis of standards recommended by the Alberta Feed and Soil Testing Laboratory for annual crops, nitrogen and phosphorus but not potassium seem to be limiting to plant growth (Pers. comm., D. Lavery).

It was necessary to correct the soil moisture data for time by referring to the soil moistures recorded on a weekly basis at the environmental station situated about 1 mile away on a comparable site. Thus, all soil moisture percentages recorded in this intensive site were corrected to 27 August as in the following example.

Soil moisture (wt/wt) at environmental station on

7th August = 4.3%

Soil moisture (wt/wt) at environmental station on

27th August = 13.0%

Difference = 8.7%

Soil moisture; stand 66, 7th August = 8.3%

Corrected soil moisture, stand 66,

7th August = $8.3 + 8.7 = 17.0\%$

However, the soil moisture and soil temperature results obtained from stand 64 were discarded as the time differences were considered too great.

The highest mean soil moisture percentages at 20 cm were recorded in the soils of the depressions (stands 66 and 71) and the lowest was in stand 70 on the N-facing

slope, but the difference was only about 6% (Table 12; Fig. 27). Soil moisture calculated as a percentage of the <2 mm fraction (*i.e.*, corrected for gravel content) differed markedly from soil moisture percentage calculated on total soil basis, as soils in low-lying areas had low gravel contents. The highest soil moistures on the <2 mm basis were in stands 65 and 70 and the lowest in 66 and 67.

Soil temperatures at 20 cm were corrected for time in the same way as soil moistures. The highest soil temperatures were on the S-facing slopes (Nos. 65, 67, 68) or on the top of the ridge (No. 69) and by far the lowest temperature was recorded in the gully (stand 71) (Table 12). Soil temperature in stand 70 on the N-facing slope was 2 F higher than in stand 71 due, presumably, to the much lower soil moisture in the former site.

10. Correlations Between Vegetation and Environment

The preceding section has described the composition and structure of the vegetation in an intensively studied area of *Festuca-Danthonia* Prairie in the Waterton Badlands. Some of the major environmental factors influencing this grassland type have also been considered. Section 10 attempts to relate the vegetation to the environment on a quantitative basis.

The quadrat observations taken as individual sampling units are suitable for this purpose. The following data were

TABLE 12. SOIL TEMPERATURE AND MOISTURE DATA FROM 20 GRASSLAND
STANDS SAMPLED IN 1968.

Stand	Mean Soil Temperature °F ¹	Mean Soil Moisture % ²	Mean Soil Moisture % of <2mm fraction ²
Henry House Intensive Study Site			
52	57.6	11.0	11.1
53	57.1	9.5	9.6
54	52.2	4.0	4.1
55	50.2	3.6	3.7
56	60.4	1.8	1.8
57	56.4	3.7	3.7
Hay Meadow Intensive Study Site			
58	55.1	18.8	20.0
59	56.0	22.2	22.9
60	52.6	27.2	28.0
61	55.8	28.2	33.2
62	61.1	7.0	12.2
63	63.4	13.9	23.2
Badlands Intensive Study Site			
64	58.9	7.3	16.9
65	57.7	17.2	28.7
66	55.2	17.5	21.5
67	55.8	15.3	22.5
68	57.1	15.9	24.4
69	56.9	17.1	24.5
70	54.8	13.6	28.7
71	52.7	19.8	25.9

Footnotes: ¹ At 20-23 cm depth at 12 noon on date of sampling; corrected for time using soil temperatures at Jasper (for Henry House) or Waterton (for Hay Meadow and Badlands) environmental stations as standards.

² As footnote 1, substituting "moisture" for "temperature".

available from five quadrats in each stand: 50 cover points for plant cover; soil temperatures and moisture at 20 cm; gravel content at 20 cm. Slope angle and aspect and elevation were calculated from stand data for each quadrat.

Thus, a number of quantitative variables pertaining to the abundance of the Dominants, to topography and to soils could be tested for correlations by Pearson's correlation coefficient, " r ", which gives a measure of the degree of association between pairs of variables but does not imply any causal relationship.

Computer techniques were used to calculate " r " values between variables Nos. 1 to 8 and 19 to 25 listed in Table 13, by using the data from five quadrats from each of stands 65 to 71 inclusive, *i.e.*, 35 observations on each variable. These coefficients are shown in matrix form in Table 14. Positive or negative correlation was considered significant at the 5% probability level.

A serious limitation of the Pearson correlation coefficient is that it does not take into account the simultaneous effects of other factors on the two correlated ones. An unknown third factor may affect both variables in such a way that their correlation is high. As the environment is a network of interacting factors, simple correlation cannot determine which of the complex of factors has the greatest effect on the vegetative attribute under study.

Multiple regression analysis to some extent overcomes these difficulties by building an equation relating the

TABLE 13. VEGETATIONAL ATTRIBUTES AND ENVIRONMENTAL VARIABLES
USED IN SIMPLE CORRELATION AND IN MULTIPLE REGRESSION
ANALYSIS OF INTENSIVE STUDY SITE DATA.

1. *Festuca scabrella* Cover, %.
2. *Danthonia parryi* Cover, %.
3. *Festuca idahoensis* Cover, %.
4. *Danthonia intermedia* Cover, %.
5. *Selaginella densa* Cover, %.
6. *Lupinus sericeus* Cover, %.
7. *Galium boreale* Cover, %.
8. Total angiosperm Cover, %¹
9. *Poa pratensis* Cover, %.
10. *Smilacina stellata* Cover, %.
11. *Stipa columbiana* Cover, %.
12. *Agropyron dasystachyum* Cover, %.
13. *Koeleria cristata* Cover, %.
14. *Calamagrostis montanensis* Cover, %.
15. *Arctostaphylos uva-ursi* Cover, %.
16. *Elymus innovatus* Cover, %.
17. *Peltigera canina* Cover, %.
18. *Antennaria nitida/rosea*² Cover, %.
19. Gravel at 20 cm, %.
20. Slope angle in degrees.
21. Slope aspect³.
22. Elevation⁴.
23. Soil temperature at 20-23 cm, in degrees Fahrenheit.
24. Soil moisture at 20-23 cm, %.
25. Soil moisture at 20-23 cm, %, calculated on the basis of
the <2 mm fraction.
26. Total herb and dwarf shrub cover, %.
27. Total shrub cover, %.
28. Total tree cover, %.

Footnotes: ¹ For correlations between total angiosperm cover and single species cover, the value "Total angiosperm cover-species cover" was used.

² Sampling confusion resulted in combined cover values.

³ Given numerical values as follows: N = 5, NE and NW = 4, E, W, and flat = 3, SE and SW = 2, and S = 1.

⁴ Height in feet above the lowest point in the study area.

selected variable (dependent variable) to a number of other variables which may influence it (independent variables) (Smillie, 1965). In step-wise multiple regression, these independent variables are selected in order of the magnitude of their correlation with the dependent variable. Before the addition of each new term to the equation, the influence of the independent variables previously included is removed from the variation of the dependent variable. In this way, the residual variation in the dependent variable is progressively reduced and the equation can be terminated when the addition of further terms does not significantly reduce the residual variation. The final equation describes the apparent relative influence of each selected environmental factor on the selected vegetation attribute, independently of the simultaneous influence of the other environmental factors. Also, predictions can be made regarding the dependent variable if data on the independent variables are available.

The general form of the regression equation is as follows:

$$Y = A + B_1 X_1 + B_2 X_2 + B_3 X_3 - - - - B_n X_n$$

where $X_1 \dots X_n$ = independent variables

Y = dependent variable

A = equation constant

B = regression coefficient

Regression equations were terminated when the addition of another term did not reduce the sum of squares of the dependent variable by a significant amount at the 5% level.

For this purpose, a Partial F-test (Analysis of Variance) was made after the addition of each term, *i.e.*, $F = \text{Sum of squares reduced in the step/residual variation of the dependent variable}$. Also, the significance of each regression coefficient in the equation can be tested at each step by means of a Student t-test. Thus, any independent variable in the equation that becomes insignificant because of interactions with other terms subsequently added can be detected and deleted.

The step-wise multiple regression analyses were carried out by means of program No. CS101 from the program library of the Department of Computing Science, University of Alberta.

Eight regression equations were constructed relating total angiosperm cover and seven of the major species of the *Festuca-Danthonia* Prairie on the Badlands area to the environment. Eight multiple regression equations were computed with variables 1 to 8 (Table 13) as dependent variables Y_1 to Y_8 , and variables 8, and 19 to 25 in Table 13 as independent variables X_8 , and X_{19} to X_{25} in each equation.

In some cases, it was clear that the relationship between the dependent and independent variables might not be linear. Some of the independent variables were transformed as appropriate and both transformed and untransformed values were included in the regression as independent variables. The analysis procedure then selected which of these accounted for a greater proportion of the variation in the dependent variable. Transformations on variables X_8 , and X_{19} to X_{25} were calculated as follows:

Untransformed	Transformed
X_8	X_8 — cover of the species used as dependent variable in place of X_8 in equations Y_1 to Y_4 , Y_6 and Y_7
X_{19}	$\sqrt{X_{19}}$
X_{20}	cosine X_{20}
X_{21}	no transformation
X_{22}	no transformation
X_{23}	X_{23}^2 and $\log_{10} X_{23}$
X_{24}	X_{24}^2 and $\log_{10} X_{24}$
X_{25}	X_{25}^2 , $\log_{10} X_{25}$ X_{25} — Permanent Wilting Percent- age, $(X_{25} - \text{Permanent Wilting Percent-}$ $\text{age})^2$ $\log_{10} (X_{25} - \text{Permanent Wilting}$ $\text{Percentage})$

Full details of the eight multiple regression equations are given in Table 15.

(a) Interspecific and inter-environmental correlations.

Only two of the 21 interspecific pairings and seven of the 28 environmental pairings were significantly correlated at the 5% probability level. *Selaginella densa* was negatively correlated with *Festuca scabrella* and *Danthonia intermedia*.

Soils with high gravel content were negatively correlated

TABLE 15. BADLANDS INTENSIVE STUDY SITE. MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATION BETWEEN EIGHT VEGETATIONAL ATTRIBUTES AND THE SIGNIFICANT ENVIRONMENTAL VARIABLES.

<i>Festuca scabrella</i> Cover (Y_1)		Constant = -1694.8	TVA = 64.3%
<u>X</u>	<u>r</u>	<u>B</u>	<u>V</u>
Slope aspect	+0.587	7.29	34.5
$\sqrt{\text{Gravel}}$	-0.553	-4.88	20.3
Cosine slope angle	+0.288	1727.25	9.5
<i>Danthonia parryi</i> Cover (Y_2)		Constant = -2391.3	TVA = 35.3%
Total angiosperm cover - Y_2	-0.273	-0.107*	7.4
(Soil temperature) ²	-0.195	-0.820	17.4
Soil temperature	-0.186	88.92	10.5
<i>Festuca idahoensis</i> Cover (Y_3)		Constant = -4100.3	TVA = 46.0%
(Soil temperature) ²	+0.436	0.010	19.0
Elevation	-0.346	-0.067*	8.6
Cosine slope angle	+0.251	4069.9	4.5
Slope angle	-0.131	4.2	6.0
(Soil moisture) ²	+0.072	0.021	7.9
<i>Danthonia intermedia</i> Cover (Y_4)		Constant = 2920.9	TVA = 48.7%
(Soil moisture) ²	+0.371	0.189	13.8
Slope aspect	+0.333	0.294*	8.7
Soil moisture	+0.334	-6.56	4.5
Elevation	-0.321	-0.176	9.1
Slope angle	-0.194	-3.48	3.5
Cosine slope angle	+0.076	-2854.3	9.1
<i>Selaginella densa</i> Cover (Y_5)		Constant = 31.02	TVA = 70.2%
Total angiosperm cover	-0.794	-0.214	63.0
Slope aspect	-0.710	-2.80	7.2

TABLE 15. Cont'd.

<i>Lupinus sericeus</i>			
Cover (Y_6)	Constant = 58.0		TVA = 16.9%
Log_{10} soil moisture	-0.411	-43.20	16.9
<i>Galium boreale</i>			
Cover (Y_7)	Constant = 14.4		TVA = 12.0%
Log_{10} (soil moisture on <2 mm basis - PWP)	-0.346	-9.21	12.0
Total Angiosperm			
Cover (Y_8)	Constant = -1752.87		TVA = 74.1%
Soil temperature	-0.645	-3.74	41.6
Slope aspect	+0.633	11.06	20.0
$\sqrt{\text{Gravel}}$	-0.594	-5.90	7.8
Cosine slope angle	+0.193	2042.2	4.7

Notes: General form of the multiple regression equation

$$Y = A + B_1X_1 + B_2X_2 + B_3X_3 + \dots + B_nX_n$$

Where A = equation constant; B_1, B_2 , etc. = regression coefficients;

Y = dependent variable; X_1, X_2 , etc. = independent variables.

TVA = Total variation of the dependent variables accounted for by the regression %.

V = Variation of the dependent variable accounted for by the independent variable (%).

* - indicates that this regression coefficient has been made insignificant, at the 5% probability level, by the addition of subsequent terms.

r = Pearson correlation coefficient between X and Y.

with soil moisture calculated on a total soil basis but were positively correlated with soil moisture calculated on the basis of the <2 mm fraction. The higher the gravel content, the lower the <2 mm fraction, and therefore, the less the moisture required to keep this latter fraction moist.

The positive correlation between gravel content and soil temperature indicates that soils on warm, S-facing slopes and ridge tops have thinner Ah horizons and tend to have their fines fraction removed by erosion. These dry, gravelly areas have a low rate of evapotranspiration and therefore higher soil temperatures.

The negative correlation between slope aspect and elevation is not considered meaningful and is due merely to the topography in this particular area (Fig. 24).

(b) Vegetation and Environment

Total angiosperm cover was correlated positively with slope aspect and negatively with gravel content and soil temperature. The multiple regression equation of total angiosperm cover had four significant terms and accounted for 71% of the variation in this variable. One of these four terms—slope angle—did not appear as a simple correlation. Thus, there is more angiosperm cover on the cooler, N-facing slopes and on level areas, where the soils are low in gravel. The three significant terms in the multiple regression equation of *Festuca scabrella* cover, namely slope

angle, slope aspect, and gravel content, account for 64% of the variation in the mean cover of this species. This equation confirms the results of simple correlation, *i.e.*, that *Festuca scabrella* is more abundant on cooler, N-facing slopes and in depressions where the soil generally has little gravel.

Elevation and soil temperature, although significantly correlated with the dependent variable did not appear in the equation, owing to their strong positive correlation with variables previously included. No soil moisture variables appeared either in the equation or as simple correlations.

The three significant terms in the equation of *Danthonia parryi* cover accounted for only 35% of the variation in the dependent variable and therefore were inadequate to explain the environmental preferences of this species. This species, although not significantly correlated with any of the environmental variables measured, seems to be most influenced by total angiosperm cover and soil temperature. It is more tolerant of the xeric conditions on S-facing slopes and ridge tops than is *Festuca scabrella*.

Five terms in the equations of *Festuca idahoensis* accounted for only 46% of the variation in its cover; one of these terms—elevation—lost its significance when subsequent terms were added. The only sampled factors influencing *F. idahoensis* were soil temperature, slope angle and soil moisture. Their influence was, however, rather weak.

F. idahoensis seems to be most abundant on level areas where extremes of soil moisture and temperature occur less frequently. It is less abundant in the cool, mesic areas where *Festuca scabrella* and *Danthonia intermedia* are Dominant, and also in the most exposed areas where *Selaginella densa* is the major xerophyte.

Only 49% of the variation in *Danthonia intermedia* cover was accounted for by the six terms in the multiple regression equation. It does not, therefore, adequately explain the distribution and abundance of this species.

The positive correlation of *Danthonia intermedia* with slope aspect and soil moisture, together with the appearance of slope angle and elevation as negative terms in the equation, verify that it occurs with *Festuca scabrella* on N-facing slopes and in depressions (p. 157). It appears to require high soil moisture as this variable appeared prominently in the equation. It seems to tolerate shading and crowding by much larger species such as *Festuca scabrella* but cannot tolerate xeric conditions.

The equation of *Selaginella densa* cover accounted for 70% of the variation, but contained only two terms—total angiosperm cover and slope aspect. Both these variables were strongly and negatively correlated with *Selaginella*, and this species was also positively correlated with soil temperature and elevation. *Selaginella densa* occurs mainly on the warmer, S-facing slopes and on the higher, more exposed areas. It seems to be excluded from the more mesic areas

dominated by *Festuca scabrella* and other tall forbs and grasses.

The equations of both *Lupinus sericeus* and *Galium boreale* cover had only one significant term each, which accounted for only 17% and 12% respectively of their covers. These equations do not, therefore, adequately explain the distributions of the species.

Both species seem slightly more abundant in areas with lower soil moisture contents but this correlation is not statistically significant in the case of *Galium*. The positive correlation of *Lupinus* with gravel content was not confirmed by the equation, due to the negative correlation between gravel content and soil moisture. *Lupinus* and *Galium* are distributed over the whole of the Badlands intensive study site and seem to have a wide tolerance of local environmental variations.

In conclusion, it appears that *Selaginella* and the four grasses used as dependent variables in these equations form a continuum based on a complex of factors which together determine moisture availability. Thus, *Festuca scabrella* and *Danthonia intermedia* are more abundant in the more mesic sites such as depressions and N-facing slopes, while *Danthonia parryi* is more abundant in slightly less mesic sites, and *Festuca idahoensis* in xeric sites. None of the four grasses can tolerate the conditions in the most xeric and often eroded sites on exposed S-facing slopes

where *Selaginella densa* is abundant.

The average variation of the dependent variables accounted for by these eight equations was only 46%. The efficiency of these equations could probably be increased by more accurate measurements of the environmental variables, especially soil temperature and moisture, and by the introduction of variables involving long-term methods designed to sample the environment on a year-round basis, *e.g.*, the direction and speed of prevailing winds; the pattern of snow accumulation.

Waterton Grass Meadows and Sedge Meadows

1. Vegetation and Soils

Grass Meadows and Sedge Meadows occupy flat, low-lying areas in the bottoms of the main valleys of Waterton Lakes National Park, usually close to lakes and rivers. The four stands taken as examples of these meadows (Nos. 9, 60, (Grass) 10, 61, (Sedge) are on an alluvial fan which slopes very gently ($<1^\circ$) down to the S end of Knight's Lake.

The Dominant species and comments on their use by grazing animals are listed on page 107-8. Species with a mean cover of 3% or more were *Poa pratensis* (19.6) *Festuca elatior* (15.3), *Bromus inermis* (7.8), *Phleum pratense* (4.8), *Carex praegracilis* (5.9), *Juncus balticus* (3.3); *Taraxacum officinale* (10.0), *Ranunculus acris* (12.0), *Fragaria virginiana* var. *glauca* (4.8), *Aster laevis* var. *geyeri* (3.5),

Trifolium repens (3.4) and *Galium boreale* (3.4). Many species prominent in stands 9 and 60 were also prominent in the *Poa pratensis*-*Smilacina* Meadows, e.g., *Poa pratensis*, *Stipa columbiana*, *Geum triflorum*, *Smilacina stellata* and *Vicia americana*, and it is probable that the latter Meadows are transitional between *Festuca-Danthonia* Prairie and the Grass Meadows represented by Nos. 9 and 60.

The conspicuous bunch grasses which dominate the *Festuca-Danthonia* Prairie are generally absent, and most of the Dominant grasses and sedges are rhizomatous. The only stratum in these Meadows consisted of all the forbs and graminoid species, was of maximum height 50-70 cm and corresponded to the two upper strata of the *Festuca-Danthonia* Prairie.

Since many of the Dominant species have been introduced into these Meadows by horses and man, and since most other low-lying meadows in Waterton Lakes National Park have also been disturbed, there is no way of determining their stability or their original species composition. They are very limited in area and, if left undisturbed, could be succeeded by willow scrub or aspen groves which occupy similar topographic sites in the valley bottoms.

The soil horizon data are shown in condensed form in Table 6, p. 123. The soils were identified as Orthic Black Chernozems and had well-drained, slightly gravelly profiles of a sandy-loam texture. Gravel content increased with depth and there was a well-defined, loose layer of coarse

gravel at a depth between 16 and 42 inches (41 and 107 cm).

On July 3, 1967 in stands 9 and 10, and on June 24, 1968 in stand 61, the water table was at the top of the gravel layer. In No. 60, the water table was below 40 inches (102 cm) although the gravel began at 26 inches (66 cm) and the soil appeared to be very moist.

A layer of charcoal was found at 4-5 inches (10-13 cm) in stand 61.

On July 3, 1967 the soil moisture values at 9 inches (23 cm) in both Nos. 9 and 10 were below the PWP whereas on June 24, 1968 the soils in Nos. 60 and 61 were a little above FC. This further emphasizes the difference in moisture availability between the summers of the two years.

At 3 inches (8cm) depth, the soils of Nos. 9 and 60, the Grass Meadows, were almost neutral, with pH values of 6.9 and 6.8 respectively. No free lime was present at 3 inches but there were small amounts lower in the profile. In this respect, the soils of Nos. 9 and 60 resembled many of those of the *Festuca-Danthonia* Prairie. The soils of Nos. 10 and 61 (Sedge Meadows) were distinctly alkaline at 3 inches, with pH values of 7.8 and 8.0 respectively, and the profile of No. 61 had free lime almost to the surface.

Available nitrogen at 3 inches in July, 1967 in Nos. 9 and 10 was the highest recorded in this study (20.5 and 24.5 ppm). However, values were very low in Nos. 60 and 61 in June, 1968 (1.5 and 1 ppm). It appears that, during the dry summer of 1967, the available nitrogen

supply of these soils was not exhausted nearly so quickly as it was in the wet summer of 1968.

Available phosphorus and potassium were slightly higher in Nos. 9 and 60 than in Nos. 10 and 61, but were of similar magnitude in each stand in the two years. Available phosphorus but not available potassium was probably limiting to plant growth in all four stands.

The higher water table, higher pH and the presence of free lime almost to the surface all indicate that more water movement occurs in the Sedge Meadow stands (Nos. 10 and 61) than in the nearby Grass Meadow stands (Nos. 9 and 60).

2. Intensive Study of the Hay Meadow Area

The Hay Meadow is on an alluvial fan at the N end of Knight's Lake in Waterton Lakes National Park, in an area of transition from *Festuca-Danthonia* Prairie to Grass and Sedge Meadow. It was therefore suitable for a comparative ecological study of these three vegetation types. The terrain is nearly flat with a slope of less than 1° down to the lake.

Between June 21 and June 27, 1968, the following six superficially uniform stands were sampled: two relatively xeric *Festuca-Danthonia* Prairie stands (62 and 63), one Sedge Meadow stand (61) and three vegetationally intermediate stands (58, 59, 60) (Fig. 28).

Stands 59, 60 and 61 were inside the Hay Meadow enclosure but did not seem to have been cut for hay in

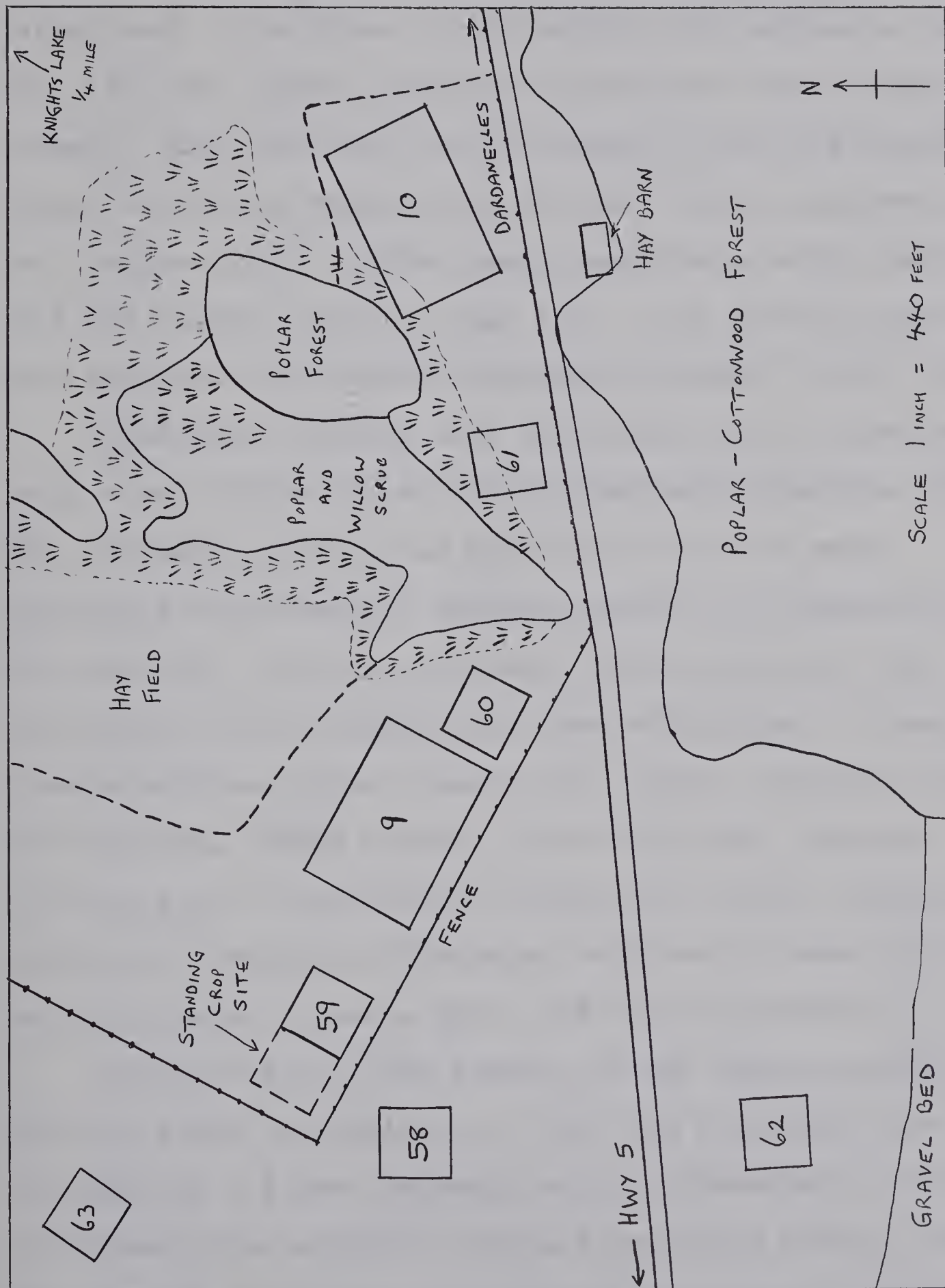


FIG. 28 HAY MEADOW INTENSIVE STUDY SITE, WATERTON LAKES NATIONAL PARK,
SHOWING STANDS 9, 10, 58-63, ——— APPROXIMATE LIMIT OF SUMMER HAY AREA.
~~~~~ SEDGE MARSH



recent years. Five horses were kept in the enclosure during summer, 1968 but did not appear to utilise the actual stand areas much. The three stands outside the enclosure (Nos. 58, 62, 63) were lightly grazed by outfitters' horses during the summer. Mule deer and, in the winter, a few elk browse and graze in the Hay Meadow area but have little apparent effect on the grassland. Pellet group counts were very similar in all six stands (Table 7, page 145). The grazing intensity was therefore considered reasonably constant in all six.

Prominence Indices were calculated for all species in each stand (Table 16) as for the Badlands intensive area (p. 157). The following species had mean PIs of 10.0 or more:

*Agropyron dasystachyum*, *Festuca elatior*, *F. idahoensis*, *F. scabrella*, *Koeleria cristata*, *Phleum pratense*, *Poa pratensis*, *Stipa columbiana*; *Carex heliophila*, *C. praegracilis*, *Juncus balticus*; *Aster laevis* var. *geyeri*, *Fragaria virginiana* var. *glauca*, *Galium boreale*, *Geum triflorum*, *Monarda fistulosa* var. *menthaefolia*, *Ranunculus acris*, *Smilacina stellata*, *Taraxacum officinale*; *Selaginella densa*; *Cornicularia aculeata*, *Cladonia* spp.; and *Tortula ruralis*.

With the aid of the results of the *Festuca-Danthonia* Prairie stand ordination (p. 132), the six stands were arranged in a linear sequence which represented a vegetation continuum from xerophytic *Festuca-Danthonia* Prairie (Nos. 62, 63) through mesophytic *Poa pratensis-Smilacina* Meadows (Nos. 58, 59), to Grass Meadows (No. 60) and Sedge Meadows (No. 61).





TABLE 16. VEGETATION STRUCTURE AND POPULATION SIZES OF THE HAY MEADOW INTENSIVE STUDY SITE.

Prominence Indices (Cover x  $\sqrt{\text{Frequency}}$ ) of all species with mean values of 0.5 or more, and Cover (%) of vegetation strata; another 2 shrubs, 1 dwarf shrub, 12 grasses and sedges and rushes, 38 forbs, 2 horsetails and 4 lichens were also recorded and have been listed in Appendices 4 and 5.

|                                                       | Stand | 62   | 63   | 58   | 59   | 60    | 61    | Mean  |
|-------------------------------------------------------|-------|------|------|------|------|-------|-------|-------|
| Total Angiosperm Cover, %.                            |       | 35.0 | 77.8 | 89.2 | 84.2 | 115.2 | 111.2 |       |
| Shrub Cover, %.                                       |       | 0.0  | 0.2  | 0.4  | 0.0  | 0.4   | 1.2   |       |
| <i>Salix bebbiana</i>                                 |       | 0    | 0    | 0    | 0    | 1     | 8     | 1.5   |
| <i>Rosa woodsii</i>                                   |       | 1    | 1    | 1    | 1    | 0     | 0     | 0.7   |
| Graminoid Cover, %.                                   |       | 18.3 | 58.8 | 59.6 | 57.4 | 61.6  | 76.8  |       |
| <i>Poa pratensis</i>                                  |       | 0    | 0    | 140  | 240  | 356   | 1     | 122.8 |
| <i>Carex heliophila</i>                               |       | 0    | 247  | 92   | 63   | 1     | 0     | 67.2  |
| <i>Stipa columbiana</i>                               |       | 3    | 20   | 98   | 100  | 23    | 1     | 60.8  |
| <i>Festuca elatior</i>                                |       | 0    | 0    | 0    | 0    | 14    | 224   | 59.7  |
| <i>Festuca idahoensis</i>                             |       | 31   | 105  | 126  | 36   | 8     | 0     | 51.0  |
| <i>Carex praegracilis</i>                             |       | 0    | 0    | 1    | 3    | 30    | 234   | 44.7  |
| <i>Juncus balticus</i>                                |       | 0    | 0    | 1    | 1    | 0     | 150   | 25.3  |
| <i>Agropyron dasystachyum</i>                         |       | 42   | 10   | 42   | 26   | 15    | 0     | 22.5  |
| <i>Festuca scabrella</i>                              |       | 33   | 67   | 27   | 5    | 0     | 0     | 22.0  |
| <i>Koeleria cristata</i>                              |       | 53   | 45   | 27   | 2    | 1     | 0     | 21.3  |
| <i>Phleum pratense</i>                                |       | 0    | 0    | 0    | 1    | 53    | 36    | 15.0  |
| <i>Bromus inermis</i>                                 |       | 0    | 0    | 0    | 0    | 50    | 1     | 8.5   |
| <i>Glyceria striata</i>                               |       | 0    | 0    | 0    | 0    | 0     | 42    | 7.0   |
| <i>Agropyron trachycaulum</i> var. <i>unilaterale</i> |       | 0    | 0    | 7    | 24   | 10    | 0     | 6.8   |
| <i>Danthonia intermedia</i>                           |       | 0    | 20   | 0    | 6    | 0     | 0     | 4.3   |
| <i>Danthonia parryi</i>                               |       | 0    | 21   | 3    | 0    | 0     | 0     | 4.0   |
| <i>Muhlenbergia richardsoni</i>                       |       | 0    | 1    | 1    | 7    | 15    | 0     | 4.0   |
| <i>Carex scirpoidea</i> var. <i>scirpiformis</i>      |       | 0    | 1    | 1    | 1    | 1     | 17    | 3.5   |





TABLE 16. Cont'd.

|                                                   | Stand | 62   | 63   | 58   | 59   | 60   | 61   | Mean |
|---------------------------------------------------|-------|------|------|------|------|------|------|------|
| <i>Bromus pumpellianus</i>                        |       | 0    | 0    | 6    | 13   | 0    | 0    | 3.2  |
| <i>Carex lasiocarpa</i> var. <i>latifolia</i>     |       | 0    | 0    | 0    | 0    | 0    | 16   | 2.7  |
| <i>Helictotrichon hookeri</i>                     |       | 1    | 1    | 3    | 0    | 1    | 0    | 2.0  |
| <i>Juncus saximontanus</i>                        |       | 0    | 0    | 0    | 0    | 0    | 8    | 1.3  |
| <i>Carex aurea</i>                                |       | 0    | 0    | 0    | 0    | 1    | 4    | 0.8  |
| <i>Agropyron spicatum</i>                         |       | 1    | 4    | 0    | 0    | 0    | 0    | 0.8  |
| <i>Hierochloe odorata</i>                         |       | 0    | 0    | 0    | 4    | 0    | 0    | 0.7  |
| Forb Cover, %.                                    |       | 16.7 | 18.8 | 29.2 | 26.8 | 53.2 | 33.2 |      |
| <i>Galium boreale</i>                             |       | 6    | 36   | 44   | 40   | 46   | 1    | 28.8 |
| <i>Taraxacum officinale</i>                       |       | 1    | 1    | 1    | 0    | 86   | 84   | 28.8 |
| <i>Smilacina stellata</i>                         |       | 0    | 0    | 42   | 114  | 7    | 6    | 28.2 |
| <i>Geum triflorum</i>                             |       | 0    | 1    | 93   | 27   | 16   | 0    | 22.8 |
| <i>Fragaria virginiana</i> var. <i>glauca</i>     |       | 0    | 0    | 0    | 1    | 98   | 11   | 18.3 |
| <i>Ranunculus acris</i>                           |       | 0    | 0    | 0    | 1    | 1    | 104  | 17.7 |
| <i>Aster laevis</i> var. <i>geyeri</i>            |       | 0    | 0    | 0    | 4    | 86   | 5    | 15.8 |
| <i>Monarda fistulosa</i> var. <i>menthaefolia</i> |       | 0    | 0    | 5    | 19   | 36   | 0    | 10.0 |
| <i>Achillea millefolium</i>                       |       | 1    | 8    | 10   | 15   | 18   | 0    | 8.7  |
| <i>Agoseris glauca</i>                            |       | 1    | 3    | 0    | 0    | 48   | 0    | 8.7  |
| <i>Cerastium arvense</i>                          |       | 18   | 6    | 16   | 1    | 1    | 0    | 7.0  |
| <i>Trifolium repens</i>                           |       | 0    | 0    | 0    | 0    | 0    | 42   | 7.0  |
| <i>Arnica sororia</i>                             |       | 1    | 33   | 1    | 1    | 0    | 0    | 6.0  |
| <i>Vicia americana</i>                            |       | 0    | 0    | 1    | 1    | 30   | 0    | 5.5  |
| <i>Antennaria umbrinella</i>                      |       | 8    | 20   | 0    | 0    | 1    | 0    | 4.8  |
| <i>Phlox hoodii</i>                               |       | 18   | 9    | 0    | 0    | 0    | 0    | 4.5  |
| <i>Geranium viscosissimum</i>                     |       | 0    | 0    | 20   | 5    | 1    | 0    | 4.3  |
| <i>Lomatium macrocarpum</i>                       |       | 23   | 3    | 0    | 0    | 0    | 0    | 4.3  |
| <i>Zygadenus gramineus</i>                        |       | 9    | 15   | 0    | 0    | 0    | 0    | 4.0  |
| <i>Thalictrum venulosum</i>                       |       | 0    | 0    | 0    | 0    | 14   | 8    | 3.7  |
| <i>Anemone</i> spp. <sup>2</sup>                  |       | 4    | 14   | 1    | 1    | 1    | 0    | 3.5  |
| <i>Chrysopsis villosa</i>                         |       | 1    | 1    | 12   | 3    | 1    | 0    | 3.0  |



TABLE 16. Cont'd.

| Stand                                             | 62   | 63   | 58  | 59  | 60  | 61  | Mean |
|---------------------------------------------------|------|------|-----|-----|-----|-----|------|
| <i>Gaillardia aristata</i>                        | 6    | 10   | 0   | 0   | 1   | 1   | 3.0  |
| <i>Solidago missouriensis</i>                     | 0    | 1    | 1   | 10  | 3   | 0   | 2.5  |
| <i>Allium textile</i>                             | 9    | 2    | 1   | 1   | 1   | 0   | 2.3  |
| <i>Potentilla gracilis</i>                        | 1    | 1    | 1   | 0   | 6   | 5   | 2.3  |
| <i>Pedicularis groenlandica</i>                   | 0    | 0    | 0   | 0   | 0   | 13  | 2.2  |
| <i>Lithospermum ruderale</i>                      | 0    | 0    | 9   | 2   | 1   | 0   | 2.0  |
| <i>Senecio indecorus</i>                          | 0    | 0    | 10  | 1   | 1   | 0   | 2.0  |
| <i>Sedum stenopetalum</i>                         | 10   | 0    | 0   | 0   | 0   | 0   | 1.7  |
| <i>Zygadenus elegans</i>                          | 0    | 1    | 0   | 0   | 0   | 8   | 1.5  |
| <i>Arenaria serpyllifolia</i>                     | 7    | 0    | 0   | 0   | 0   | 0   | 1.2  |
| <i>Oxytropis sericea</i> var. <i>spicata</i>      | 6    | 1    | 0   | 0   | 0   | 0   | 1.2  |
| <i>Astragalus agrestis</i>                        | 0    | 0    | 0   | 0   | 6   | 0   | 1.0  |
| <i>Astragalus decumbens</i> var. <i>serotinus</i> | 3    | 3    | 0   | 0   | 0   | 0   | 1.0  |
| <i>Zizia aptera</i>                               | 0    | 0    | 0   | 1   | 1   | 4   | 1.0  |
| <i>Calochortus apiculatus</i>                     | 1    | 1    | 1   | 0   | 1   | 1   | 0.8  |
| <i>Eriogonum caespitosus</i>                      | 3    | 1    | 1   | 0   | 0   | 0   | 0.8  |
| <i>Eriogonum flavum</i>                           | 5    | 0    | 0   | 0   | 0   | 0   | 0.8  |
| <i>Trifolium pratense</i>                         | 0    | 0    | 0   | 0   | 0   | 5   | 0.8  |
| <i>Campanula rotundifolia</i>                     | 0    | 1    | 0   | 1   | 2   | 0   | 0.7  |
| <i>Comandra pallida</i>                           | 4    | 0    | 0   | 0   | 0   | 0   | 0.7  |
| <i>Crepis runcinata</i>                           | 0    | 0    | 0   | 0   | 0   | 4   | 0.7  |
| <i>Lathyrus ochroleucus</i>                       | 0    | 0    | 0   | 0   | 3   | 1   | 0.7  |
| <i>Senecio canus</i>                              | 1    | 1    | 1   | 1   | 0   | 0   | 0.7  |
| <i>Erysimum inconspicuum</i>                      | 1    | 1    | 0   | 1   | 0   | 0   | 0.5  |
| <i>Saxifraga occidentalis</i>                     | 0    | 3    | 0   | 0   | 0   | 0   | 0.5  |
| <i>Sisyrinchium montanum</i>                      | 0    | 0    | 0   | 1   | 1   | 1   | 0.5  |
| <i>Pteridophyte</i> Cover, %.                     | 6.0  | 18.7 | 0.0 | 0.0 | 0.2 | 0.0 |      |
| <i>Selaginella densa</i>                          | 54   | 187  | 0   | 0   | 0   | 0   | 40.2 |
| <i>Bryophyte</i> Cover, %.                        | 15.3 | 26.0 | 0.0 | 0.0 | 0.0 | 5.0 |      |
| <i>Tortula ruralis</i>                            | 124  | 253  | 0   | 0   | 0   | 13  | 65.0 |
| <i>Bryum</i> spp.                                 | 25   | 4    | 0   | 0   | 0   | 4   | 5.5  |
| <i>Brachythecium salebrosum</i>                   | 0    | 0    | 0   | 0   | 0   | 6   | 1.0  |





TABLE 16. Cont'd.

|                              | Stand | 62   | 63  | 58  | 59  | 60  | 61  | Mean |
|------------------------------|-------|------|-----|-----|-----|-----|-----|------|
| Lichen Cover, %.             |       | 14.5 | 4.4 | 0.0 | 0.2 | 0.0 | 0.0 |      |
| <i>Cladonia</i> spp.         | 65    | 30   | 0   | 0   | 1   | 0   | 0   | 16.0 |
| <i>Cornicularia aculeata</i> | 62    | 6    | 0   | 0   | 0   | 0   | 0   | 11.3 |
| <i>Physcia muscigena</i>     | 11    | 1    | 0   | 0   | 0   | 0   | 0   | 2.0  |
| <i>Peltigera canina</i>      | 6     | 2    | 0   | 0   | 0   | 0   | 0   | 1.3  |

Footnotes: <sup>1</sup> Includes *Anemone multifida* and *A. patens* var. *wolfgangiana*



The grassland structure across the continuum became more simplified towards the Sedge Meadow end. Stands 62 and 63 had the three-strata structure of the *Festuca-Danthonia* Prairie, although the tall forb-bunch grass was poorly represented. In stands 58 and 59, the strata were less well-defined but the tall forb-bunch grass stratum was much better represented. In stands 60 and 61, only one stratum was apparent.

The mean PIs of the Dominant species were plotted on this continuum to show their maximum abundance (Fig. 29). The PIs of *Festuca idahoensis*, *F. scabrella*, *Koeleria cristata*, *Carex heliophila*, *Selaginella densa* and *Tortula ruralis* were maximal in the *Festuca-Danthonia* Prairie stands, and *Lomatium macrocarpum*, *Phlox hoodii*, *Cornicularia aculeata* and *Physcia muscigena* were especially prominent in No. 62, the most xeric stand.

The Prominence Indices of the following species were maximal in the *Poa pratensis-Smilacina* Meadow stands: *Agropyron trachycaulum* var. *unilaterale*, *Stipa columbiana*, *Chrysopsis villosa*, *Geranium viscosissimum*, *Geum triflorum*, *Lithospermum ruderales*, *Senecio indecorus* and *Smilacina stellata*.

Species with Prominence Indices maximal in the Grass Meadow stand were *Bromus inermis*, *Muhlenbergia richardsonis*, *Phleum pratense*, *Poa pratensis*, *Agoseris glauca*, *Aster laevis* var. *geyeri*, *Fragaria virginiana* var. *glauca*, *Monarda fistulosa* var. *menthaefolia*, *Taraxacum officinale* and *Vicia*



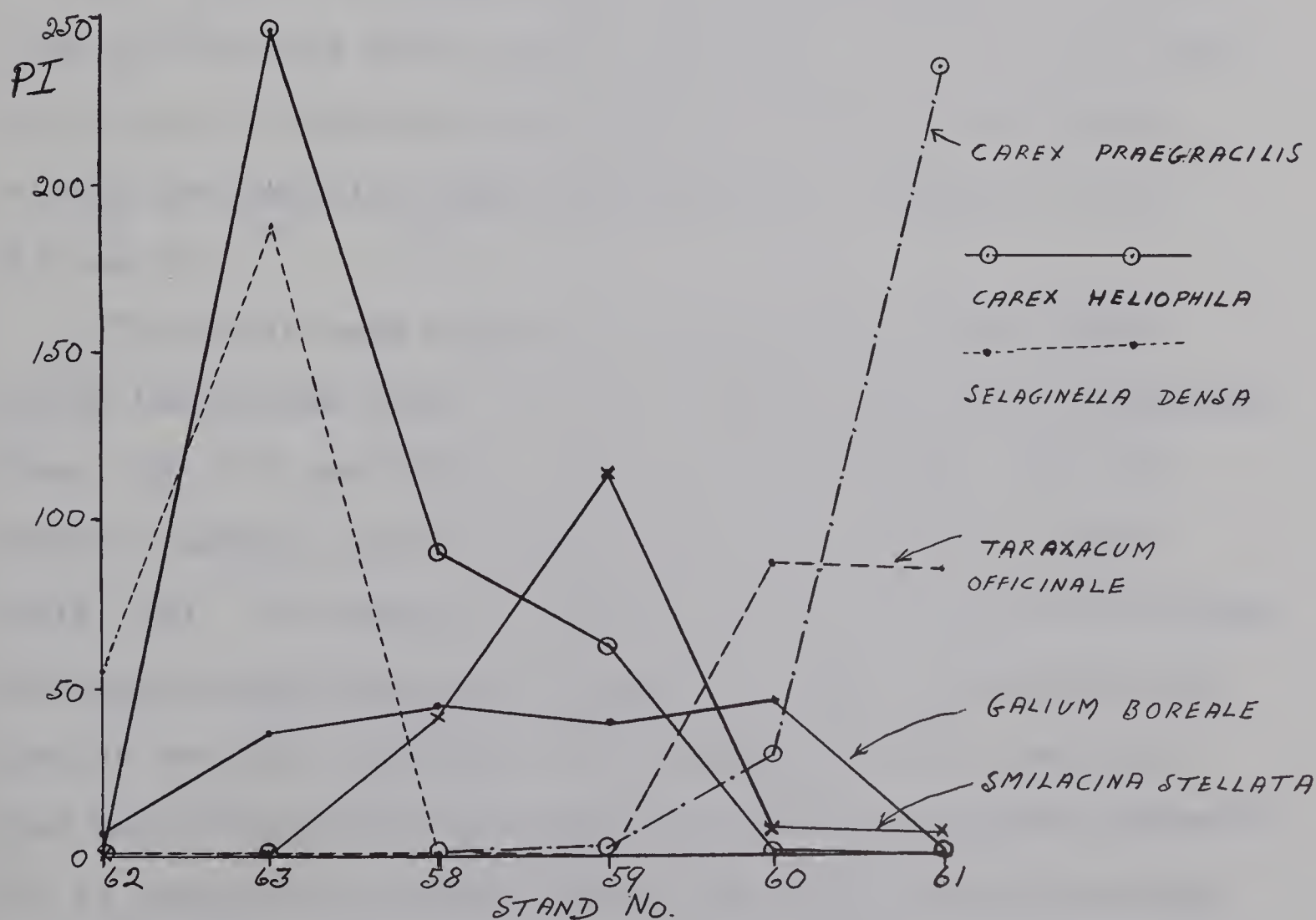
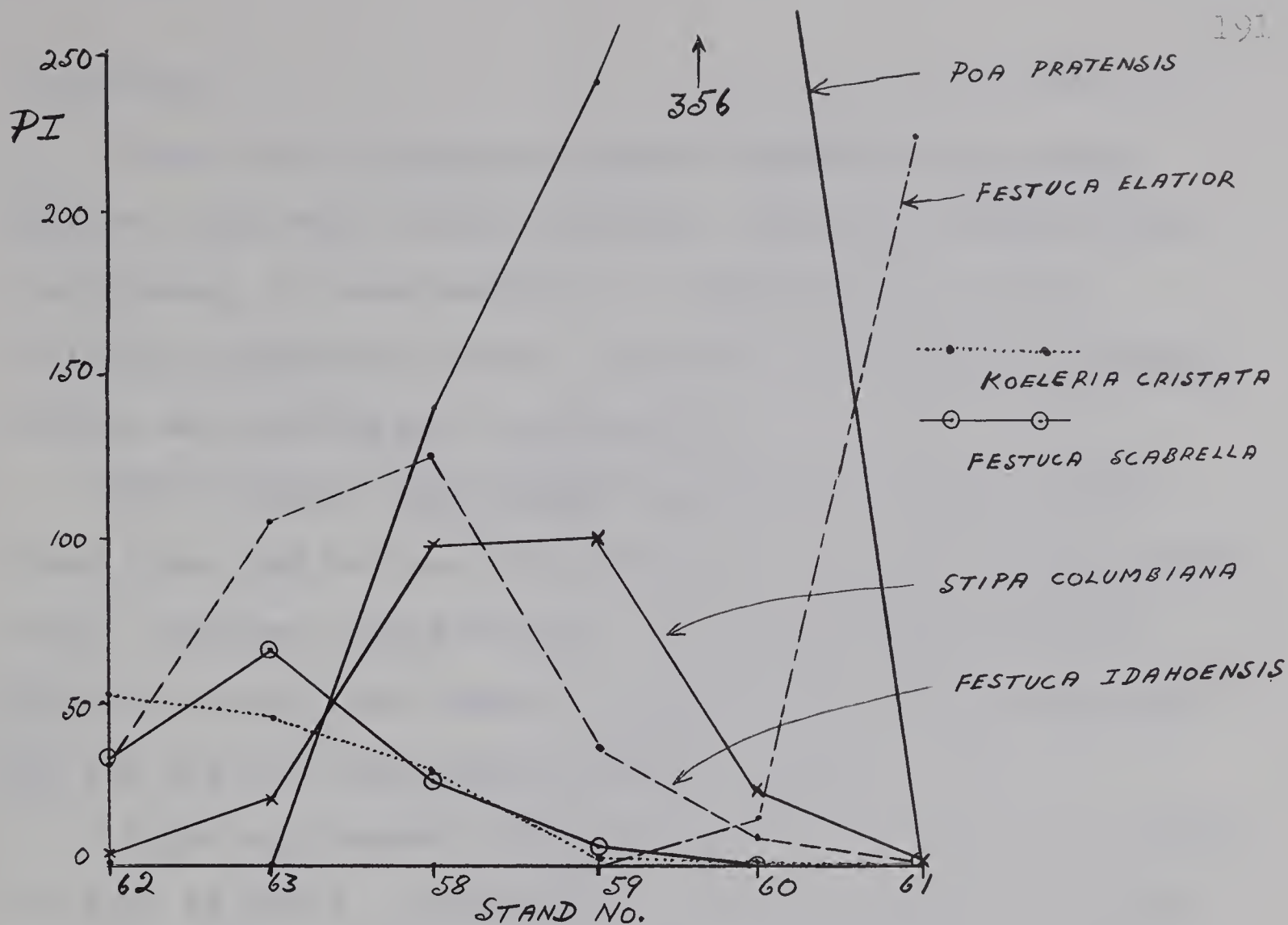


FIG. 29 PROMINENCE INDICES OF 12 SELECTED SPECIES  
IN THE HAY MEADOW INTENSIVE STUDY SITE, WATERTON





*americana*.

Those with Prominence Indices maximal in the Sedge Meadow stand were *Festuca elatior*, *Glyceria striata*, *Carex lasiocarpa*, *C. praegracilis*, *C. scirpiformis*, *Juncus balticus*, *Ranunculus acris*, *Taraxacum officinale*, *Trifolium repens* and *Pedicularis groenlandica*.

Most species were highly specific to certain grass-land types and not one was prominent across the whole continuum. *Agropyron dasystachyum*, *Achillea millefolium* and *Galium boreale* were common in all of the stands except No. 61 and did not have marked maximum values.

Total angiosperm cover was lowest in No. 62 and highest in Nos. 60 and 61, indicating a trend to greatest standing crop on the more moist sites (Fig. 30). On the other hand, the cover of combined pteridophytes, mosses and lichens showed the opposite trend and reached a maximum in Nos. 62 and 63.

The soils were tentatively identified as Rego Dark Brown Chernozems (Nos. 62, 63), Orthic Dark Brown Chernozems (Nos. 58, 59) and Orthic Black Chernozems (Nos. 60, 61). Gravel content varied considerably from stand to stand (Fig. 30). In Stands 62 and 63, below the 5-8 cm Ah horizon the soils had high gravel contents, sandy <2 mm fractions, and no obvious structure. In stands 58 to 61, the soils had much thicker Ah horizons (13-23 cm), low gravel contents to at least 66 cm, sandy-loam <2 mm fractions and distinct B horizons.



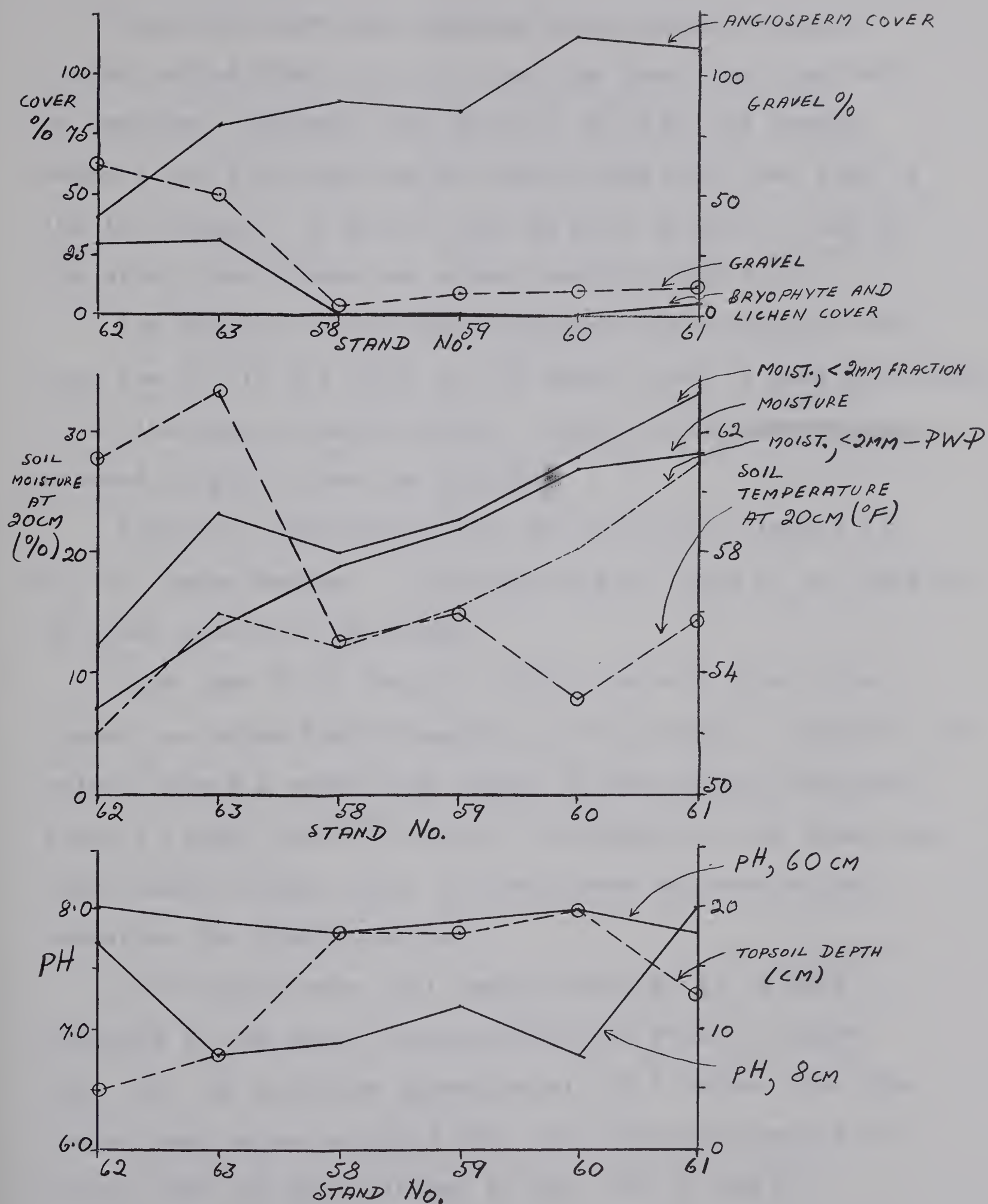


FIG. 30 VEGETATIONAL ATTRIBUTES AND ENVIRONMENTAL VARIABLES IN THE HAY MEADOW INTENSIVE STUDY SITE





The soils were all alkaline below the Ah horizon; the pH varied from 7.8 to 8.3 and the free lime from "nil" to "medium". However, the pH at 8 cm in No. 61 (Sedge Meadow) was 8.0; this was the only stand with free lime in the Ah horizon. In No. 62, the pH at 8 cm was 7.6 and in the other four stands was almost neutral (6.7-7.2).

The amounts of available nitrogen and phosphorus were very low in all six soils at all depths (not >5 ppm) and seemed to be limiting to plant growth. In No. 61 the amounts increased slightly down the profile.

Available potassium in the Ah horizon was lowest in No. 61 (Sedge Meadow). Potassium did not seem to be limiting to plant growth in any stand.

From June 22 to June 27, 1968, the soil in all six stands was above Field Capacity at 20 cm depth. However, the values showed a trend from lowest in the *Festuca-Danthonia* Prairie stands (Nos. 62 and 63) to highest in the Grass and Sedge Meadow stands (Fig. 30) both when uncorrected and corrected for gravel content.

The highest mean soil temperatures at 20 cm were recorded in the xeric *Festuca-Danthonia* Prairie stands (Nos. 62, 63) and were approximately 10 F higher than the lowest mean value recorded (No. 60) and approximately 6 F higher than the temperatures in Nos. 58, 59 and 61.



### 3. Correlations Between Vegetation and Edaphic Factors

In the preceding section, the floristic composition and vegetation structure of the Hay Meadow intensive site, and influential edaphic variables have been described. Vegetation will now be related to environment on a quantitative basis.

The quadrat data were suitable for this purpose. The same data were available from five quadrats in each of the six stands (*i.e.*, 30 observations on each variable) as for the Badlands intensive study site (p. 166), except that no topographic variables were included as the terrain was essentially flat. Only eight species were present in enough of the 30 quadrats to warrant their inclusion (variables 1, 3, 7, 9-13) in Table 13, p. 169. Only one value each for soil nutrients, pH and free lime was available for each stand. These values were not, therefore, used in correlations.

Pearson correlation coefficients ("*r*") were calculated between variables Nos. 1, 3, 7-13, 19, 23-25 listed in Table 13 and the results shown in matrix form in Table 17. Positive or negative correlations were considered significant at the 5% probability level.

Nine multiple regression equations were computed as for the Badlands intensive site (p. 171). Variables 1, 3, 7-13 in Table 13 were used as dependent variables,  $Y_1 - Y_9$ , and variables 8, 19 and 23-25 as independent









variables,  $X_8$ ,  $X_{19}$ ,  $X_{23}$  -  $X_{25}$ . The same transformations on the independent variables were calculated as for the multiple regression on p. 173 and were also included in the equation as independent variables. Full details of the nine equations are given in Table 18.

(a) Interspecific and inter-environmental correlations

Only 6 of the 28 interspecific pairings were significantly correlated at the 5% probability level. *Festuca scabrella* and *Koeleria cristata* were positively correlated with each other but were negatively correlated with species which have their greatest abundance in the moister stands. Thus, both species were negatively correlated with *Poa pratensis*. *Koeleria* was also negatively correlated with *Smilacina stellata*.

*Stipa columbiana* was positively correlated with *Festuca idahoensis* and *Poa pratensis*. The remaining two species, *Agropyron dasystachyum* and *Galium boreale*, were not correlated with any other species.

Soil temperature, the two soil moisture variables, gravel content and total angiosperm cover were all strongly correlated with each other, *i.e.*, all five of the independent variables in the multiple regression equations were dependent on each other. Lower temperatures were recorded in soils with higher moisture and lower gravel contents. Soil moisture calculated on the basis of the



TABLE 18. HAY MEADOW INTENSIVE STUDY SITE, MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATION BETWEEN NINE VEGETATIONAL ATTRIBUTES AND THE SIGNIFICANT ENVIRONMENTAL VARIABLES.

|                                                       |          |                       |             |
|-------------------------------------------------------|----------|-----------------------|-------------|
| <i>Poa pratensis</i><br>Cover ( $Y_1$ )               |          | Constant = -12393.5   | TVA = 81.4% |
| <u>X</u>                                              | <u>r</u> | <u>B</u>              | <u>V</u>    |
| Log <sub>10</sub> soil temperature                    | -0.732   | 13137.1               | 53.6        |
| (Soil temperature) <sup>2</sup>                       | -0.711   | 1.42                  | 14.5        |
| Total angiosperm<br>Cover - $Y_1$                     | +0.202   | -0.235                | 10.0        |
| Soil temperature                                      | -0.722   | -267.6                | 3.3         |
| <i>Festuca idahoensis</i><br>Cover ( $Y_2$ )          |          | Constant = -322.7     | TVA = 73.1% |
| (Soil moisture,<br><2 mm basis-PWP) <sup>2</sup>      | -0.408   | 0.618                 | 16.6        |
| Log <sub>10</sub> (soil moisture,<br><2 mm basis)     | -0.154   | 97.90*                | 11.3        |
| Soil moisture, <2<br>mm basis-PWP                     | -0.317   | -27.94                | 23.2        |
| Log <sub>10</sub> (soil moisture,<br><2 mm basis-PWP) | -0.084   | -24.22*               | 4.0         |
| (Soil moisture,<br><2 mm basis) <sup>2</sup>          | -0.352   | -0.666                | 12.2        |
| Soil moisture,<br><2 mm basis                         | -0.272   | 37.51                 | 5.8         |
| <i>Festuca scabrella</i><br>Cover ( $Y_3$ )           |          | Constant = -13.73     | TVA = 49.4% |
| (Soil temperature) <sup>2</sup>                       | +0.591   | 0.002*                | 34.9        |
| (Soil moisture) <sup>2</sup>                          | -0.569   | -0.009                | 5.0         |
| Log (soil moisture,<br><2 mm basis)                   | -0.250   | 11.02                 | 9.5         |
| <i>Galium boreale</i><br>Cover ( $Y_4$ )              |          | no significant terms. |             |
| <i>Smilacina stellata</i><br>Cover ( $Y_5$ )          |          | Constant = 10.79      | TVA = 37.3% |
| $\sqrt{\text{Gravel}}$                                | -0.492   | -1.25                 | 24.2        |
| Total angiosperm<br>Cover - $Y_5$                     | +0.055   | -0.050                | 13.5        |





TABLE 18. Cont'd.

|                                                       |            |         |             |
|-------------------------------------------------------|------------|---------|-------------|
| <i>Stipa columbiana</i>                               |            |         |             |
| Cover ( $Y_6$ )                                       | Constant = | 14.08   | TVA = 45.4% |
| $\sqrt{\text{Gravel}}$                                | -0.521     | -1.81   | 27.2        |
| (Soil moisture) <sup>2</sup>                          | +0.022     | -0.009  | 18.2        |
| <i>Agropyron dasystachyum</i>                         |            |         |             |
| Cover ( $Y_7$ )                                       | Constant = | 6.61    | TVA = 26.3% |
| Soil moisture,<br><2 mm basis-PWP                     | -0.513     | -0.226  | 26.3        |
| <i>Total Angiosperm</i>                               |            |         |             |
| Cover ( $Y_8$ )                                       | Constant = | 965.5   | TVA = 77.4% |
| $\text{Log}_{10}$ soil moisture                       | +0.818     | 75.3    | 66.9        |
| $\text{Log}_{10}$ soil temper-<br>ature               | -0.811     | -555.3  | 10.5        |
| <i>Koeleria cristata</i>                              |            |         |             |
| Cover ( $Y_9$ )                                       | Constant = | -27.06  | TVA = 73.8% |
| Soil moisture                                         | -0.764     | -4.13   | 58.4        |
| (Soil temperature) <sup>2</sup>                       | +0.728     | 0.0005* | 6.4         |
| $\text{Log}_{10}$ (soil moisture,<br><2 mm basis-PWP) | -0.498     | 1.95*   | 1.0         |
| (Soil moisture) <sup>2</sup>                          | -0.726     | 0.021   | 1.4         |
| $\text{Log}_{10}$ soil moisture                       | -0.746     | 27.30   | 6.6         |

For explanation of terms and symbols, see footnotes to Table 15, p.174.



<2 mm fraction still showed a strong negative correlation with gravel content c.f. Badlands intensive study site results (p. 176). This indicates that the <2 mm fractions were drier in gravelly than in non-gravelly soils.

(b) Vegetation and environment

The correlation of total angiosperm cover with all four environmental variables measured indicates that the soils of the drier, gravelly areas (*e.g.*, stands 62 and 63) which have higher maximum temperatures, develop soil moisture deficits more quickly than those in the moister areas and so support less vegetation.

However, in the multiple regression equation of total angiosperm cover, two terms, soil temperature and moisture, accounted for most of the variation (77%). Angiosperm cover is therefore highest on cooler, moister soils and is evidently less affected by gravel content.

The three significant terms in the equation of *Festuca scabrella* cover accounted for only 49% of the variation in the cover of this species. The addition of the two soil moisture terms reduced the soil temperature term to insignificance. In the Hay Meadow area, *Festuca scabrella* is more abundant on the drier soils, which have higher daytime temperatures. It seems to be less affected by gravel content of the soil or by total cover, although it is strongly correlated with both.



Although *Festuca idahoensis* was not significantly correlated with any of the edaphic factors measured, the six-term, multiple regression equation of this species cover accounted for 73% of its variation. All six terms were soil moisture variables, and it seems that *Festuca idahoensis* occurs most abundantly on the drier sites in the Hay Meadow area. The lack of a significant correlation with total angiosperm cover indicates that *Festuca idahoensis* is not excluded from the moister sites by competition from taller-growing species, but rather by some factor connected with the soil moisture régime.

The five-term equation of *Koeleria cristata* cover accounted for 74% of the variation of this species. Four of these terms were soil moisture variables, and the soil temperature term became insignificant. In the Hay Meadow area, it seems that *Koeleria* is primarily influenced by soil moisture. It can tolerate low soil moisture, and has, therefore, a competitive advantage over most of the other grasses on the drier sites.

There were four significant terms in the equation of *Poa pratensis* cover. Three soil temperature terms accounted for 71%, and the whole equation accounted for 81% of the variation in the cover of this species. The strong positive correlation between *Poa pratensis* and gravel content did not appear in the equation, because of the inter-environmental correlations mentioned previously (p. 197). It appears that *Poa pratensis* occurs predominantly on soils with low





temperature maxima and cannot tolerate the high temperatures associated with drier sites in Waterton.

The two terms in the equation of *Smilacina stellata* cover accounted for only 37% of the variation in the dependent variable. *Smilacina stellata* seems to be more abundant on soils with low gravel content. Although this species had no significant correlations with soil temperature or moisture, it is more abundant in areas with high angiosperm cover. This suggests that its distribution is influenced by some undetermined factor or factors which favor angiosperm cover.

The two terms in the equation for *Stipa columbiana* cover accounted for only 45% of the variation in the dependent variable. *Stipa columbiana*, like *Smilacina*, is more abundant on soils with low gravel contents. Unlike *Smilacina*, however, it is more abundant on the moister soils and seems unaffected by total angiosperm cover.

The sole significant term in the equation of *Agropyron dasystachyum* accounted for only 26% of the variation. This species seems to be a little more abundant on the drier soils in the Hay Meadow area but is apparently unaffected by local variations in soil temperature, gravel content or total cover.

No equation could be computed for *Galium boreale* cover as neither the Partial F-test nor the regression coefficients had any significant values at the 5% probability level. This species seems to have a wide range of



tolerance of the edaphic factors measured and of total cover.

The environmental conditions in the Hay Meadow area do not appear to be optimum for the *Festuca-Danthonia* Prairie Dominants such as *Festuca idahoensis* and *F. scabrella* which appear to occupy habitats quite different from those of the same species in the Badlands area. In the Hay Meadow area, they occur on the drier sites but in the Badlands area *Festuca scabrella* is most abundant in the moister sites while *F. idahoensis* is fairly evenly distributed. The exclusion of both *Festuca* species from the moister Hay Meadows areas seems attributable to excessive soil moisture rather than to competition, but it is possible that both are excluded by some other factor, such as difficulty of establishment.

*Agropyron dasystachyum* and *Koeleria cristata* are both primarily influenced by soil moisture and seem to represent a group of opportunist species which can grow in sites in this area too dry for the usual Dominant species.

Since 18 of the 21 soil moisture and temperature variables appearing in the equations are transformations, most of the correlations presented are not linear. The value of these transformations is clear. However, no transformation seemed more generally useful than the rest and the type of transformation used for each independent variable has, therefore, to be determined with reference to each particular dependent variable.





Koeleria-Calamagrostis montanensis Grasslands

1. Vegetation, Topography and Soils

The Dominant, Constant and Differential species of this grassland type are listed on p. 108-9. These grasslands characteristically have low species diversity and low total cover of vascular plant species (approximately 80%). The mean number of vascular species per stand ( $60,000 \text{ ft}^2 = 5,574 \text{ m}^2$ ) was only 31. Only five species had mean cover values of 3% or more: *Calamagrostis montanensis* (4.4), *Koeleria cristata* (10.7), *Antennaria nitida/rosea*<sup>1 2</sup> (18.1), *Artemisia frigida* (6.4) and *Astragalus striatus* (5.0).

Most of the prominent species in this grassland were low-growing and few were taller than 23 cm. Thus, there is no "tall forb-bunch grass" stratum *c.f.* *Festuca-Danthonia* Prairie at Waterton (Plate 2).

The only species more than 23 cm high were scattered small shrubs, chiefly *Rosa woodsii* and *Potentilla fruticosa* which were present in a few stands. There are two rather ill-defined strata in these grasslands, which are similar to the two lower strata in the *Festuca-Danthonia* Prairie and have a number of species in common with them. These strata are (a) a "low grass-forb" stratum of 25 cm or less in height in which the most prominent species are *Agropyron*

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<sup>1 2</sup> See footnote, p. 59







(a)



(b)

Plate 2.

- (a) *Koeleria-Calamagrostis montanensis* Grassland: stand 42, Jasper National Park; heavily grazed by elk in winter and early spring (July, 1967).
- (b) Detailed view of *Koeleria-Calamagrostis montanensis* Grassland; stand 43, Jasper National Park; shows the sparse ground cover. *Erigeron caespitosus* is prominent (July, 1967).



*dasystachyum*, *Bromus pumpellianus*, *Calamagrostis montanensis*, *Koeleria cristata*, *Poa interior*; *Carex eleocharis*; *Anemone multifida*, *A. patens* var. *wolfgangiana*, *Astragalus striatus*, *Artemisia frigida*, *Erigeron caespitosus*, *Gaillardia aristata*, *Galium boreale*, *Linum lewisii*, *Oxytropis sericea* var. *spicata*, *Senecio cymbalarioides* and *Solidago decumbens*.

(b) a mat-like ground cover (less than 5 cm high) of immature plants of the above species, together with *Antennaria nitida/rosea*,<sup>1 3</sup> *Androsace septentrionalis* and a number of crustose and foliose terricolous lichens, such as *Lecidea decipiens* and *Peltigera canina*.

The first common species to flower in 1967 and 1968 were *Anemone patens* var. *wolfgangiana*, *Androsace septentrionalis*, *Arabis holboellii* var. *retrofacta*, *Arenaria rubella*, *Draba lanceolata* and *Linum lewisii*; in 1967, these species were fruiting by June 20-23. Most of the forbs and grasses had, in 1967, begun to flower by June 20-23 and were fruiting in early July. The following prominent species, however, did not begin flowering until the middle of July: *Agropyron dasystachyum*, *Achillea millefolium*, *Antennaria nitida*, *Erigeron caespitosus*, *Gaillardia aristata*, *Potentilla pensylvanica* and *Solidago decumbens*. *Artemisia campestris* and *A. frigida* flowered last of all, in August. As in the *Festuca-Danthonia* Prairie,

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<sup>1 3</sup> See footnote, p. 59





most of the late flowering species are in the Compositae.

The following terricolous lichens were very characteristic of the more xeric sites in the *Koeleria-Calamagrostis montanensis* Grasslands: *Cladonia* spp. (mostly *C. pyxidata*), *Cornicularia aculeata*, *Lecidea decipiens*, *Peltigera canina*, *Physcia muscigena*, *Squamarina lentigera* and *Toninia coeruleonigricans*. *Lecidea*, *Physcia*, *Squamarina* and *Toninia*, together with colonies of the blue-green alga *Nostoc* sp., were especially prominent in the overgrazed and wind-eroded stands in the Athabasca River valley and were found only rarely elsewhere in this study.

The small turf mosses *Bryum* spp., *Ceratodon purpureus* and *Tortula ruralis* were common in many of the stands.

Some of the stands in the Athabasca River valley in Jasper Park represent the xerophytic extreme of this grassland type (e.g., Nos. 37, 48). The unstable, wind-eroded or-deposited soil surface supported the smallest number of species of any area in this study (No. 37 = 15, No. 48 = 24). Under these extreme environmental conditions, the prominent species were *Agropyron dasystachyum*, *Koeleria cristata*, *Artemisia frigida*, *Erigeron caespitosus* and *Salsola kali* var. *tenuifolia*.

All stands of the *Koeleria-Calamagrostis montanensis* Grassland in Jasper National Park were in the bottom of the Athabasca River valley between the E highway entrance to the Park and Jasper townsite, i.e., between 52° 55½'N and 53° 13½' N. The difference in elevation between the lowest stands



(Nos. 36, 39) and the highest (No. 37) was only 180 ft (3,245 ft elevation of lowest, 3,425 ft elevation of highest).

The two stands representing this grassland type in Banff National Park (Nos. 32, 35) were about 1,100 ft higher in elevation than any of those in Jasper but were almost 2° of latitude S of them—a partial compensation for higher elevation. This agrees very well with the Hopkins (1938) correction factor of 100 ft elevation per 15' latitude.

Fourteen of the 19 stands sampled were on level ground. Five were on slopes: Nos. 37, 42, 53 and 56 on SE-facing slopes of 12°, 2°, 1° and 3° respectively, and No. 52 on a NE-facing slope of 3°.

This grassland type occurs mainly on alluvium and alluvial fans. However, in many sites the alluvial sands and silts have been redeposited by wind, and the extensive Henry House flats area is composed of aeolian sands and silts. Stands 37 and 48, the two most xeric stands in this study, were on loess and seemed to be in an active state of wind-erosion and/or -deposition.

The soils of the *Koeleria-Calamagrostis montanensis* Grasslands were the most xeric, undeveloped and nutrient-poor of any in this study. They were all Orthic Regosols except stand 42 (Orthic Brown Wooded), stands 54, 55, 57 (Degraded Brown Wooded), and stand 32 which had 3 different types of soil profile: Orthic Regosol (on high ground), Orthic Black Chernozem (on low ground) and Orthic Brown





Wooded (near forest edge).

The Ah horizons were very thin, mostly less than 5 cm thick, and reached a maximum of 10-13 cm in the lower areas in stands 32, 45, 47 and 53. There was very little litter and the surfaces of most soils appeared to be very unstable. Nearly all the topsoils in the Athabasca River valley stands in Jasper contained considerable amounts of windblown silt and in some stands there was a structureless accumulation of loose, grey-brown silt on the surface, *e.g.*, Nos. 36, 37, 39 and 42 had about 25 cm of silt. The mean depth of stabilised windblown silt, including the thin Ah horizon, was estimated at about 13 cm in this grassland type.

The texture of the mineral soil horizons (based on weighted means to 90 cm) varied from loam to pure sand with the majority being sandy loams (Table 6, p. 123). Stand 38 had clay hardpans at 48-60 cm and 74-86 cm with a coarse, alluvial gravel layer between. No. 42 had clay loam from 64 cm down. The mean gravel content of the soil was less than 20% in all stands except Nos. 32, 39, 44 and 45 which had 66%, 47%, 44% and 29% gravel respectively.

Free lime was "medium" to "high" in all horizons of all stands. pH values were correspondingly high and generally increased with depth. The pH at 8 cm ranged from 7.9 to 8.4 except in stand 55, the pine forest stand, (7.6). The pH at 60 cm ranged from 8.1 to 9.1. Free lime content



and pH values were much higher in these grasslands than in any others in this study.

Available nutrients were generally lower than for the other grassland types. Available nitrogen and phosphorus were very low throughout all the soils ( $<4$  ppm) and generally decreased to nil in the B and C horizons, except in No. 48 where nitrogen values of 18 ppm and 12 ppm were recorded in the horizons below 38 cm. This same stand also had an unusually high sodium content (100 ppm), sulphate content ("very high") and a conductivity of 3-4 mmhos in the profile below 25 cm. These data suggest that this is a ground water discharge area.

Available potassium varied greatly from 44 ppm to 300+ ppm at 8 cm and from 7 ppm to 128 ppm at 60 cm.

Soil moisture at 23 cm in 1967 showed the same trend towards deficits in summer as those for the *Festuca-Danthonia* Prairie in Waterton Lakes National Park (Fig. 19, p. 127). On June 22-23, the soil moisture in stand 36 was already below the Permanent Wilting Percentage but in stand 37 was still above Field Capacity (the soil in the latter had a very low Field Capacity). In the period July 12-19, three of the five stands sampled were below Permanent Wilting Percentage and the other two were slightly above it. The soils sampled during August 8-13 were all close to the Permanent Wilting Percentage. In stand 35, sampled on August 30, the soil was below PWP. Thus, soil moisture deficits



at 23 cm were present in much of this grassland by early July in 1967 as in Waterton (p. 126). The summer of 1967 was drier than normal in both Banff and Jasper and precipitation figures at their Met. Stations were 3.44 and 5.51 inches respectively. These figures are 2.65 and 0.61 inches below normal<sup>14</sup> for these months.

The soils of the six stands sampled in the period June 14-18 in 1968 were all well below their Field Capacities and that of No. 52 was also below the Permanent Wilting Percentage (Fig. 20, p. 127).

## 2. Standing Crops

Two areas were sampled for standing crop in 1968. The first was an area of typical *Koeleria-Calamagrostis montanensis* Grassland on Henry House flats in Jasper Park, adjacent to stand 52. The second was close to stand 27 and to Banff airstrip. Stand 27 was only an outer satellite of cluster D (p. 97) and so cannot strictly be considered *Koeleria-Calamagrostis montanensis* Grassland. However, consideration of standing crop in this site has been included in this section for comparison with more typical sites.

Estimations of standing crop were carried out as for the *Festuca-Danthonia* Prairie site (p. 117). Student t-tests were made to determine if there was any significant difference

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<sup>14</sup> Normal value based on 30-year mean (1931-60).





in the mean standing crops of the five cones sampled on each of the two sampling dates in July and August. The results of these tests indicated that the differences were not significant at the 5% probability level (Table 5, p. 119). Therefore, the standing crop values for the two dates were combined.

At the Henry House site, the mean standing crop values for graminoids, forbs and total crop were 497, 188 and 685 kg/ha respectively, and the ranges of individual cone values were 346-662, 87-282 and 510-798 kg/ha respectively. Thus, the standing crop was much lower than at any of the *Festuca-Danthonia* Prairie sites (p. 117) and also varied less from cone to cone. Most of the standing crop at the Henry House site consisted of *Calamagrostis montanensis*, *Koeleria cristata*, *Antennaria nitida* and *Artemisia frigida*.

The species which contributed most to the standing crop at the Banff airstrip site were *Agropyron dasystachyum*, *Poa pratensis*, *Stipa richardsonii*, *Carex* spp., *Geum triflorum*, and *Taraxacum officinale*. As cluster analysis has shown, stand 27, adjacent to this site, is not closely related vegetationally to any of the other stands in this study. Although many of the Dominant species of the *Koeleria-Calamagrostis montanensis* Grasslands were present, none of them were prominent in this stand. Species composition indicates that it is intermediate between *Koeleria-Calamagrostis montanensis* Grassland and *Koeleria-Geum triflorum* Grassland, with the addition of a number of widely-distributed "invaders"



such as *Poa pratensis* and *Taraxacum officinale*. The Banff airstrip site seemed to be more mesic than the Henry House site and the standing crop was correspondingly greater. The mean standing crops of graminoids, forbs and total vegetation cover were 1,010, 456 and 1,466 kg/ha respectively and the ranges of individual cone values were 539-1,479, 84-944 and 1,228-1,751 kg/ha respectively.

Thus, there were greater ranges of values at the Banff airstrip site for graminoids and for forbs than at the Henry House site. This suggests a less uniform micro-environment at the former site. The total standing crop at the Banff airstrip site was similar to that at the heavily-grazed Upper Stoney Creek site in the *Festuca-Danthonia* Prairie in Waterton. However, grazing intensity has been much more severe at the Upper Stoney Creek site in recent years (pellet group count for stand 19, close to Upper Stoney Creek, = 160; for stand 27, = 18; for stand 52, close to Henry House, = 30). It is clear that the Henry House site and, to a lesser extent, the Banff airstrip site are far less productive than the three *Festuca-Danthonia* Prairie sites at Waterton.

### 3. Effects of Grazing

All the stands sampled in the *Koeleria-Calamagrostis montanensis* Grasslands showed moderate to heavy grazing, mostly by elk. The mean pellet group count of native ungulates for an area of 1,800 ft<sup>2</sup> (167 m<sup>2</sup>) in these stands was





67 and ranged from 153 in stand 47 to 18 in stand 32 which was inside the fence surrounding the Banff Golf Club grounds. Herds of elk descend to low elevations in the mountain parks in the fall and graze throughout the winter and early spring in the bottoms of the main valleys, where most of the *Koeleria-Calamagrostis montanensis* Grasslands are located.

Grazing by horses in these grasslands was not an important factor as the mean fecal group count for horses was only 3 in 1,800 ft<sup>2</sup> (167 m<sup>2</sup>) and the highest value recorded in any one stand was only 12 in 1,800 ft<sup>2</sup>.

A notable feature of *Koeleria-Calamagrostis montanensis* Grasslands was the almost complete absence of ground squirrels *c.f.* the *Festuca-Danthonia* Prairie, where local disturbances due to ground squirrel activity were common.

The relative contributions of elk grazing and of generally arid soil and climate to the paucity of vegetation in the *Koeleria-Calamagrostis montanensis* Grasslands can be partially assessed by the use of exclosures. Three exclosures, each 30 ft x 35 ft (9 m x 11 m), were set up in 1956 by biologists of the Canadian Wildlife Service in these grasslands, all in the Athabasca River valley in Jasper National Park. These three exclosures are at Devona, Moberly Meadows and Henry House flats (Figs. 2 and 31) and are close to stands 36, 42 and 43 respectively. These exclosures were sampled intensively in July, 1968 by Dr. D. Flook of the Canadian Wildlife Service in conjunction with the author (Flook and Stringer, manuscript in preparation)



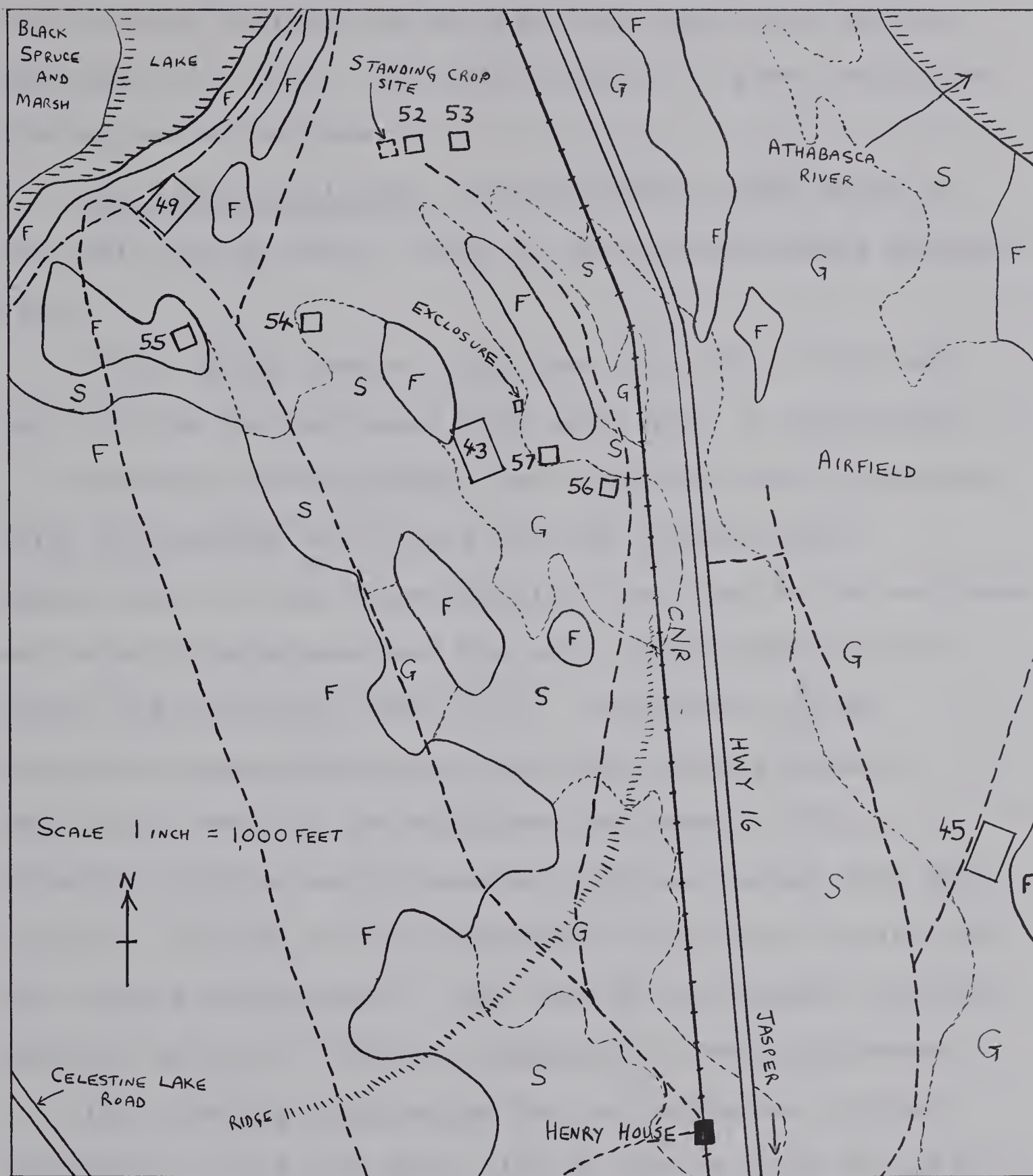


FIG. 31 HENRY HOUSE AREA, JASPER NATIONAL PARK,

SHOWING STANDS 43, 45, 49, 52-57

----- TRAILS  
 F = FOREST (CONIFEROUS)  
 S = SAVANNA  
 G = GRASSLAND





and the data analysed in the same way as for the Waterton exclosures (p. 148). The major results of these exclosure studies are as follows.

The Devona exclosure is on alluvium at the mouth of the Snake Indian River, close to the disused Devona warden's cabin.

Pellet group counts in an area of 1,000 ft<sup>2</sup> (93 m<sup>2</sup>) just outside the exclosure plot were: elk, 27 and horses, 5.

*Agropyron dasystachyum*, *Poa interior*, total graminoids, total angiosperms and litter all had significantly higher cover at the 5% probability level inside the exclosure, and culms of *Agropyron* and *Poa* were significantly taller inside the exclosure (Table 19). *Antennaria nitida*, *Potentilla pensylvanica* and *Nostoc* sp. were prominent immediately outside the exclosure but absent inside. *Artemisia frigida* and *Astragalus striatus* seemed much more prominent outside the exclosure but in neither species were the results significant. Only one of the Dominant species, *Koeleria cristata*, showed no detectable cover difference.

The standing crop inside the exclosure was (kg/ha): graminoids, 1,794 and forbs, 137 to give a total of 1,931. There were significantly higher standing crop values of *Agropyron dasystachyum*, graminoids and total angiosperms inside the plot and of *Astragalus striatus* outside the plot. *Poa interior* had much higher standing crop inside and *Artemisia frigida* more outside but the differences were not statistically significant because of large sampling variation.





TABLE 19. DEVONA EXCLOSURE PLOT.

|                                                       | Mean<br>Inside <sup>1</sup> | Mean<br>Outside <sup>1</sup> | t <sup>2</sup> |
|-------------------------------------------------------|-----------------------------|------------------------------|----------------|
| Litter Cover, %                                       | 89.5                        | 47.3                         | 9.6982**       |
| Angiosperm Cover, %                                   | 59.5                        | 46.0                         | 4.7980**       |
| Graminoid Cover, %                                    | 48.3                        | 22.0                         | 10.2470**      |
| <i>Agropyron dasystachyum</i> Cover, %                | 28.5                        | 1.0                          | 16.5831**      |
| <i>Poa interior</i> Cover, %                          | 7.3                         | 2.0                          | 3.8129**       |
| <i>Antennaria nitida</i> Cover, %                     | 0.0                         | 2.8                          | --             |
| <i>Artemisia frigida</i> Cover, %                     | 0.8                         | 4.8                          | --             |
| <i>Astragalus striatus</i> Cover, %                   | 3.8                         | 7.5                          | 1.1829         |
| <i>Potentilla pensylvanica</i> Cover, %               | 0.0                         | 4.0                          | --             |
| <i>Nostoc</i> sp. Cover, %                            | 0.0                         | 6.0                          | --             |
| <i>Agropyron dasystachyum</i> , height <sup>3</sup>   | 73.1                        | 43.5                         | 9.6490**       |
| <i>Poa interior</i> , height <sup>3</sup>             | 38.1                        | 20.8                         | 8.3368**       |
| Angiosperm standing crop, kg/ha                       | 1931                        | 869                          | 7.1831**       |
| Graminoid standing crop, kg/ha                        | 1794                        | 387                          | 23.4844**      |
| <i>Agropyron dasystachyum</i><br>standing crop, kg/ha | 1028                        | 40                           | 8.0790**       |
| <i>Koeleria cristata</i><br>standing crop, kg/ha      | 190                         | 108                          | 2.4231*        |
| <i>Poa interior</i> standing<br>crop, kg/ha           | 471                         | 41                           | 3.0121*        |
| <i>Artemisia frigida</i> standing<br>crop, kg/ha      | 13                          | 52                           | 2.0294         |
| <i>Astragalus striatus</i> standing<br>crop, kg/ha    | 25                          | 248                          | 4.5646**       |
| Soil temperature at 15 cm, °F.                        | 60.5                        | 62.8                         | 5.8931**       |
| Soil moisture at 2-5 cm, %.                           | 6.8                         | 6.1                          | 0.6831         |
| Soil moisture at 15-20 cm, %.                         | 7.0                         | 6.0                          | 0.6207         |
| Organic carbon at 2-5 cm, %.                          | 5.5                         | 6.8                          | 1.2086         |
| Organic carbon at 15-20 cm, %.                        | 2.5                         | 2.6                          | 0.2198         |

Footnotes: <sup>1</sup> - see Table 8, p.149.<sup>2</sup> - see Table 8, p.149.<sup>3</sup> - height of culms in cm; 19 degrees of freedom,  
t = 2.093 at 5% level and t = 1.729 at 10% level of  
significance.



Soil temperature was the only soil factor showing any significant difference.

The soil profile to 30 cm was similar inside and outside the exclosure, with 0-10 cm of loose, grey silt (loess) 4 cm of buried soil profile with wood charcoal, and finally compact, dark grey-brown silt down to a layer of pure sand at 23-30 cm.

Thus, although there is much greater plant cover and standing crop inside the exclosure and a distinct change in species composition, these changes have not as yet been reflected in any changes in soil characteristics.

The Moberly Meadow exclosure is about 200 ft E of the Celestine Lake Road and about 500 ft SE of the Devona area warden's headquarters in Jasper. Pellet group counts in an area of 1,000 ft<sup>2</sup> just outside the exclosure were: elk, 6 and horse, 1.

There was significantly more cover of *Calamagrostis montanensis*, total graminoids, total angiosperms and litter inside the plot (Table 20). *Astragalus striatus* and *Campanula rotundifolia* were prominent inside the plot but absent in the rest of the sampling area. *Artemisia frigida* was abundant outside the plot but absent inside. There were no detectable differences in cover of the other two prominent grasses, *Agropyron dasystachyum* and *Koeleria cristata*. Culms of *Calamagrostis montanensis*, the only grass flowering abundantly, were significantly taller inside the exclosure.

The standing crop inside exclosure was (kg/ha):





TABLE 20. MOBERLY MEADOWS EXCLOSURE PLOT.

|                                                           | Mean<br>Inside <sup>1</sup> | Mean<br>Outside <sup>1</sup> | t <sup>2</sup> |
|-----------------------------------------------------------|-----------------------------|------------------------------|----------------|
| Litter Cover, %                                           | 86.0                        | 26.8                         | 12.5200**      |
| Angiosperm Cover, %                                       | 52.3                        | 27.0                         | 5.7089**       |
| Graminoid Cover, %                                        | 34.0                        | 15.0                         | 13.4351**      |
| <i>Calamagrostis montanensis</i><br>Cover, %              | 24.8                        | 7.0                          | 5.9512**       |
| <i>Artemisia frigida</i> Cover, %                         | 0.0                         | 7.5                          | --             |
| <i>Astragalus striatus</i> Cover, %                       | 6.8                         | 0.0                          | --             |
| <i>Campanula rotundifolia</i> Cover, %                    | 4.0                         | 0.0                          | --             |
| <i>Calamagrostis montanensis</i> ,<br>height <sup>3</sup> | 10.8                        | 6.6                          | 7.1042**       |
| Angiosperm standing crop, kg/ha                           | 1067                        | 568                          | 2.8694*        |
| Graminoid standing crop, kg/ha                            | 613                         | 378                          | 2.8485*        |
| <i>Agropyron dasystachyum</i><br>standing crop, kg/ha     | 151                         | 27                           | 5.9523**       |
| <i>Calamagrostis montanensis</i><br>standing crop, kg/ha  | 358                         | 241                          | 1.9202         |
| <i>Koeleria cristata</i> standing<br>crop, kg/ha          | 85                          | 65                           | 0.7926         |
| <i>Artemisia frigida</i> standing<br>crop, kg/ha          | 0                           | 107                          | --             |
| <i>Astragalus striatus</i> standing<br>crop, kg/ha        | 190                         | 0                            | --             |
| Soil temperature at 15 cm, °F.                            | 58.5                        | 62.3                         | 6.7084**       |
| Soil moisture at 2-5 cm, %.                               | 12.5                        | 6.2                          | 5.8856**       |
| Soil moisture at 15-20 cm, %.                             | 17.4                        | 12.1                         | 8.2325**       |
| Organic carbon at 2-5 cm, %.                              | 4.8                         | 4.9                          | 0.1254         |
| Organic carbon at 15-20 cm, %.                            | 3.2                         | 1.9                          | 3.5363         |
| Permanent Wilting Percentage<br>at 2-5 cm, %.             | 13.4                        | 12.6                         | 1.0632         |
| Permanent Wilting Percentage<br>at 15-20 cm, %.           | 15.4                        | 11.1                         | 3.6899**       |

Footnotes: <sup>1</sup> - see Table 8, p.149.<sup>2</sup> - see Table 8, p.149.<sup>3</sup> - see Table 19, p.217.



graminoids, 613 and forbs, 454, to give a total of 1,067. This is considerably less than in the Devona exclosure. Only *Agropyron dasystachyum* had a significantly higher standing crop value within the plot although there were considerably higher standing crop values of graminoids and total angiosperms inside the plot.

There was a noticeable difference in the soil profile inside and outside the exclosure (*c.f.* Devona exclosure). Inside, there was a 4-6 cm Ah horizon on top of a hard, compact, light brown silt. Outside, the Ah horizon was only about 2 cm or less thick.

There was significantly more organic matter at 15-20 cm inside the plot but not at 2-5 cm. Soil moisture was significantly higher inside the plot at both depths. Soil temperature at 15 cm was lower inside the plot. The Permanent Wilting Percentage of the soil was significantly higher inside the plot at 15-20 cm, where the organic matter content was higher.

Thus, along with the higher plant cover, litter, and standing crop inside the plot, there is higher soil moisture, lower soil temperature, a deeper Ah horizon and a change in the relative abundance of some species.

The Henry House exclosure plot is on Henry House flats about  $\frac{1}{2}$  mile NW of the Canadian National Railway linesman's house.

The elk pellet group count was 8 in 1,000 ft<sup>2</sup>. There was significantly more cover of *Peltigera canina*, total





mosses (*Tortula ruralis*, *Bryum* sp. and *Ceratodon purpureus*), and more litter inside the enclosure (Table 21). Although *Koeleria cristata* had a little more cover outside and *Calamagrostis montanensis* and *Antennaria nitida* a little more cover inside the enclosure, these differences were not significant and the cover values of both graminoids and forbs were only slightly higher inside. There was no significant difference in the height of *Calamagrostis montanensis* culms.

The standing crop inside the enclosure was (kg/ha): graminoids, 367, and forbs, 344, to give a total of only 711. This is much less than in either the Devona or Moberly Meadows enclosures. *Calamagrostis montanensis* and total graminoids had significantly greater standing crops inside the enclosure. *Agropyron dasystachyum* also had greater standing crop inside the plot but the difference was not significant.

The soil profile was very similar inside and outside the plot; there were 0-6 cm of loose, grey-brown silt, then light brown, sandy silt to about 15 cm and then coarse sand to at least 30 cm. The coarse sand horizon seemed a little closer to the surface outside the plot.

The soil temperature at 15 cm was significantly lower by 3 3/4 F inside the enclosure and the following soil factors were all significantly higher inside the enclosure at the 15-20 cm depth: soil moisture %, organic matter %, Field Capacity%, Permanent Wilting Percentage and available





TABLE 21. HENRY HOUSE ENCLOSURE PLOT.

|                                                            | Mean<br>Inside <sup>1</sup> | Mean<br>Outside <sup>1</sup> | t <sup>2</sup> |
|------------------------------------------------------------|-----------------------------|------------------------------|----------------|
| Litter Cover, %.                                           | 52.3                        | 31.0                         | 5.4453**       |
| Angiosperm Cover, %.                                       | 26.8                        | 23.8                         | 1.0634         |
| Graminoid Cover, %.                                        | 13.3                        | 13.5                         | 0.1707         |
| <i>Calamagrostis montanensis</i><br>Cover, %.              | 8.0                         | 5.0                          | 2.0381         |
| <i>Koeleria cristata</i> Cover, %.                         | 4.0                         | 6.8                          | 2.9055*        |
| <i>Antennaria nitida</i> Cover, %.                         | 6.0                         | 1.8                          | 2.5726*        |
| <i>Peltigera canina</i> Cover, %.                          | 11.8                        | 1.8                          | 6.1722**       |
| Total bryophyte Cover, %.                                  | 13.8                        | 1.8                          | 6.3027**       |
| <i>Calamagrostis montanensis</i> ,<br>height. <sup>3</sup> | 8.3                         | 6.6                          | 3.9578**       |
| Angiosperm standing crop, kg/ha                            | 711                         | 519                          | 2.1744         |
| Graminoid standing crop, kg/ha                             | 367                         | 254                          | 4.6971**       |
| <i>Agropyron dasystachyum</i><br>standing crop, kg/ha      | 27                          | 3                            | 1.9160         |
| <i>Calamagrostis montanensis</i><br>standing crop, kg/ha   | 253                         | 177                          | 5.6826**       |
| <i>Koeleria cristata</i> standing<br>crop, kg/ha           | 60                          | 48                           | 1.1996         |
| <i>Antennaria nitida</i> standing<br>crop, kg/ha           | 151                         | 104                          | 0.4802         |
| <i>Artemisia frigida</i> standing<br>crop, kg/ha           | 118                         | 73                           | 1.8206         |
| Soil temperature at 15 cm, °F.                             | 71.0                        | 74.8                         | 7.8353**       |
| Soil moisture at 2-5 cm, %.                                | 4.1                         | 3.0                          | 1.8925         |
| Soil moisture at 15-20 cm, %.                              | 5.5                         | 2.8                          | 7.3647**       |
| Organic carbon at 2-5 cm, %.                               | 2.1                         | 2.1                          | 0.1502         |
| Organic carbon at 15-20 cm, %.                             | 0.7                         | 0.5                          | 2.8723*        |
| Field Capacity at 15-20 cm, %.                             | 11.9                        | 6.1                          | 6.3508**       |
| Permanent Wilting at 15-20 cm, %.                          | 4.3                         | 2.1                          | 4.9826**       |
| Available water at 15-20 cm, %.                            | 7.6                         | 4.0                          | 6.2971**       |

Footnotes: <sup>1</sup> - see Table 8, p.149.  
<sup>2</sup> - see Table 8, p.149.  
<sup>3</sup> - see Table 19, p.217.



water %. No significant difference was detected in any soil factor at the 2-5 cm depth.

Thus, a higher litter cover and standing crop of graminoids inside the exclosure are associated with a deeper and more mature soil profile.

In conclusion, grazing by elk results in a decrease of total graminoid cover and of standing crop. *Agropyron dasystachyum*, *Calamagrostis montanensis* and *Poa interior* decrease under grazing pressure whereas *Koeleria cristata* is not affected, and certain xerophytic forbs such as *Artemisia frigida* tend to increase at the expense of the grasses. The results of the exclosure study are inconsistent with regard to *Antennaria nitida* and *Astragalus striatus*. At Devona, both species have decreased when protected from grazing whereas at Henry House and Moberly Meadows, where the standing crops were much smaller, they have increased slightly. This apparent inconsistency can be resolved with reference to the relative aridity of the three sites and to the abundance of the Dominant grasses. At Henry House and, to a lesser extent, at Moberly Meadows, the very low standing crop indicates extreme aridity, and, under these conditions, it seems that even the most xerophytic species increase under grazing protection. At Devona, however, the more mesic environment permits a much greater standing crop of grasses inside the exclosure, and xerophytic forbs such as *Antennaria nitida*, *Artemisia frigida* and *Astragalus striatus*, which can better withstand the more xeric





environment and grazing pressure outside the enclosure, are competitively excluded inside it.

The pellet group counts considered in relation to the small standing crop indicate that grazing pressure can be considered excessive. Strong valley winds, coarse sandy soil, low elevation, and a rain shadow effect are instrumental in causing low precipitation/evapotranspiration ratios and hence a semi-desert or steppe type of vegetation in the Athabasca River valley; the grasslands of this valley probably have a very low carrying capacity.

#### 4. Intensive Study of the Henry House Area

The Henry House area is at latitude  $52^{\circ} 59\frac{1}{2}'$  N and longitude  $118^{\circ} 4'$  W and is approximately  $\frac{1}{2}$ - $\frac{3}{4}$  mile NNW of the Henry House Canadian National Railway siding in the Athabasca River valley in Jasper National Park. It is an area of very gently rolling terrain with very dry, sandy soils, probably of alluvial and aeolian origin, and is occupied by a mosaic of lodgepole pine forest, lodgepole pine savanna and *Koeleria-Calamagrostis montanensis* Grassland.

Six stands, each 100 ft x 100 ft, were chosen within an area of about  $\frac{1}{8}$  square mile in order to investigate the correlations between certain edaphic and topographic factors and vegetation, especially in the transition zone between pine forest and arid grassland (Fig. 31). The six stands were sampled between June 14-18, 1968, in the same



way as the Badlands intensive site (p. 44).

The six stands were of the following vegetation types: three in *Koeleria-Calamagrostis montanensis* Grassland, (Nos. 52, 53 and 56), two in lodgepole pine savanna (Nos. 54 and 57), and one in lodgepole pine forest (No. 55).

The maximum relief in the Henry House intensive area was only about 30 ft (3,390 ft - 3,420 ft), and elevational differences between stands were not measured accurately enough to make the data useful. Stands 54 and 57 were flat. Stands 53 and 55 were in slight hollows with slopes averaging about 2 degrees. Stands 52 and 56 were on 2 and 3 degree slopes facing N 60° E and S 70° E respectively.

Data on the percentage cover of trees and on the position of the stands 52-57 on the 71-stand ordination (p. 84) were used to arrange the six stands in the linear sequence 56, 52, 53, 57, 54, 55 which represents a vegetational continuum from xerophytic *Koeleria-Calamagrostis montanensis* Grassland to lodgepole pine forest. The mean Prominence Indices (p. 157) of the major plant species (Table 22), the cover of the strata, and the measured environmental variables were plotted on this continuum to show correlations with grassland, savanna or forest (Figs. 32 and 33).

The three stands with tree cover (Nos. 54, 55 and 57) had 7, 54 and 20 trees of lodgepole pine (*Pinus contorta*) in the sampling area. Cores taken from the tree nearest to the centre of each quadrat in each stand





TABLE 22. VEGETATION STRUCTURE AND POPULATION SIZES OF THE HENRY HOUSE INTENSIVE STUDY SITE.

Prominence Indices of all species with mean values of 0.5 or more, and Cover (%) of vegetation strata; another 3 shrub, 19 forbs, 3 bryophytes and 7 lichens were also recorded and have been listed in Appendices 4 and 5.

|                                                | Stand | 55   | 54   | 57   | 53   | 52   | 56   | Mean |
|------------------------------------------------|-------|------|------|------|------|------|------|------|
| Tree Cover, %.                                 |       | 32.0 | 18.0 | 13.0 | 0.0  | 0.0  | 0.0  |      |
| Total Vascular species (Understorey) Cover, %. |       | 28.6 | 36.9 | 30.8 | 40.9 | 23.5 | 27.2 |      |
| Shrub Cover, %.                                |       | 7.9  | 4.6  | 2.1  | 0.5  | 0.0  | 0.0  |      |
| <i>Shepherdia canadensis</i>                   |       | 5    | 24   | 9    | 1    | 0    | 0    | 6.5  |
| <i>Juniperus communis</i>                      |       | 28   | 1    | 1    | 1    | 0    | 0    | 5.2  |
| <i>Rosa acicularis</i>                         |       | 3    | 1    | 1    | 0    | 0    | 0    | 0.8  |
| <i>Potentilla fruticosa</i>                    |       | 0    | 0    | 0    | 3    | 1    | 0    | 0.7  |
| Dwarf shrub Cover, %.                          |       | 11.2 | 14.4 | 11.1 | 0.0  | 0.0  | 0.0  |      |
| <i>Arctostaphylos uva-ursi</i>                 |       | 100  | 144  | 78   | 0    | 0    | 0    | 53.7 |
| Graminoid Cover, %.                            |       | 8.9  | 9.0  | 17.2 | 39.5 | 21.7 | 27.2 |      |
| <i>Calamagrostis montanensis</i>               |       | 0    | 8    | 32   | 87   | 89   | 72   | 48.0 |
| <i>Koeleria cristata</i>                       |       | 3    | 31   | 39   | 56   | 18   | 70   | 36.2 |
| <i>Elymus innovatus</i>                        |       | 71   | 8    | 15   | 1    | 0    | 0    | 15.8 |
| <i>Agropyron dasytachyum</i>                   |       | 2    | 9    | 19   | 5    | 1    | 1    | 6.2  |
| <i>Bromus pumpeillianus</i>                    |       | 1    | 2    | 2    | 7    | 1    | 13   | 4.3  |
| <i>Carex filifolia</i>                         |       | 0    | 0    | 0    | 0    | 16   | 0    | 2.7  |
| <i>Poa interior</i>                            |       | 2    | 2    | 1    | 5    | 0    | 0    | 1.7  |
| <i>Festuca saximontana</i>                     |       | 1    | 5    | 1    | 2    | 0    | 0    | 1.5  |
| <i>Carex eleocharis</i>                        |       | 1    | 1    | 0    | 7    | 0    | 0    | 1.5  |
| <i>Carex richardsonii</i>                      |       | 0    | 3    | 3    | 1    | 0    | 0    | 1.2  |
| <i>Carex rossi</i>                             |       | 1    | 1    | 1    | 1    | 0    | 0    | 0.7  |
| Forb Cover, %.                                 |       | 0.6  | 8.7  | 5.2  | 22.3 | 9.1  | 11.4 |      |
| <i>Antennaria nitida/rosea</i> <sup>2</sup>    |       | 1    | 27   | 1    | 180  | 23   | 37   | 44.8 |
| <i>Antemisia frigida</i>                       |       | 1    | 1    | 8    | 1    | 11   | 22   | 7.3  |
| <i>Senecio cymbalarioides</i>                  |       | 1    | 7    | 5    | 1    | 22   | 1    | 6.2  |
| <i>Anemone</i> spp. <sub>1</sub>               |       | 3    | 11   | 6    | 4    | 1    | 4    | 4.8  |





TABLE 22. Cont'd.

|                                                         | Stand | 55  | 54  | 57  | 53  | 52  | 56  | Mean |
|---------------------------------------------------------|-------|-----|-----|-----|-----|-----|-----|------|
| <i>Solidago decumbens</i>                               |       | 3   | 6   | 8   | 4   | 2   | 5   | 4.7  |
| <i>Campanula rotundifolia</i>                           |       | 1   | 5   | 1   | 16  | 1   | 0   | 4.0  |
| <i>Artemisia campestris</i>                             |       | 1   | 1   | 1   | 1   | 3   | 16  | 3.8  |
| <i>Erigeron caespitosus</i>                             |       | 1   | 1   | 1   | 0   | 1   | 9   | 2.2  |
| <i>Astragalus agrestis</i>                              |       | 0   | 0   | 0   | 11  | 1   | 0   | 2.0  |
| <i>Astragalus tenellus</i>                              |       | 1   | 1   | 1   | 2   | 6   | 1   | 2.0  |
| <i>Galium boreale</i>                                   |       | 1   | 6   | 1   | 1   | 1   | 0   | 1.7  |
| <i>Astragalus striatus</i>                              |       | 1   | 2   | 3   | 1   | 0   | 1   | 1.3  |
| <i>Linum lewisii</i>                                    |       | 1   | 1   | 1   | 1   | 3   | 1   | 1.3  |
| <i>Gaillardia aristata</i>                              |       | 1   | 1   | 1   | 0   | 1   | 1   | 0.8  |
| <i>Oxytropis sericea</i> var. <i>spicata</i>            |       | 1   | 1   | 1   | 1   | 1   | 0   | 0.8  |
| <i>Androsace septentrionalis</i>                        |       | 0   | 1   | 1   | 1   | 0   | 1   | 0.7  |
| <i>Arabis holboellii</i> var. <i>retrofracta</i>        |       | 0   | 1   | 1   | 1   | 1   | 0   | 0.7  |
| <i>Draba lanceolata</i>                                 |       | 1   | 1   | 0   | 1   | 1   | 0   | 0.7  |
| <i>Viola adunca</i>                                     |       | 1   | 1   | 0   | 1   | 0   | 0   | 0.5  |
| Terricolous Bryophyte Cover, %.                         |       | 1.4 | 0.4 | 1.0 | 2.8 | 0.0 | 1.8 |      |
| <i>Bryum</i> sp. <sup>2</sup>                           |       | 1   | 2   | 7   | 24  | 0   | 15  | 8.2  |
| <i>Ceratodon purpureus</i> <sup>2</sup> (same as above) |       |     |     |     |     |     |     |      |
| <i>Brachythecium salebrosum</i>                         |       | 4   | 1   | 0   | 0   | 0   | 0   | 0.8  |
| <i>Tortula ruralis</i>                                  |       | 1   | 1   | 0   | 0   | 0   | 1   | 0.5  |
| Terricolous Lichen Cover, %.                            |       | 0.0 | 1.1 | 1.4 | 3.9 | 1.5 | 2.0 |      |
| <i>Peltigera canina</i>                                 |       | 1   | 8   | 10  | 39  | 2   | 13  | 12.2 |
| <i>Physcia muscigena</i>                                |       | 0   | 0   | 1   | 0   | 6   | 3   | 1.7  |
| <i>Lecidea decipiens</i>                                |       | 0   | 0   | 1   | 0   | 1   | 1   | 0.5  |
| <i>Squamarina lentigera</i>                             |       | 0   | 0   | 1   | 0   | 1   | 1   | 0.5  |
| <i>Toninia coeruleonigricans</i>                        |       | 0   | 0   | 1   | 0   | 1   | 1   | 0.5  |
| Terricolous Algae Cover, %.                             |       | 0.0 | 0.1 | 0.7 | 0.1 | 2.4 | 1.6 |      |
| <i>Nostoc</i> sp.                                       |       | 0   | 1   | 4   | 1   | 25  | 15  | 7.7  |

Footnotes: <sup>1</sup> - Includes *Anemone multifida* and *A. patens* var. *wolfgangiana*.

<sup>2</sup> - Sampling confusion between these two species resulted in a combined Prominence Index.



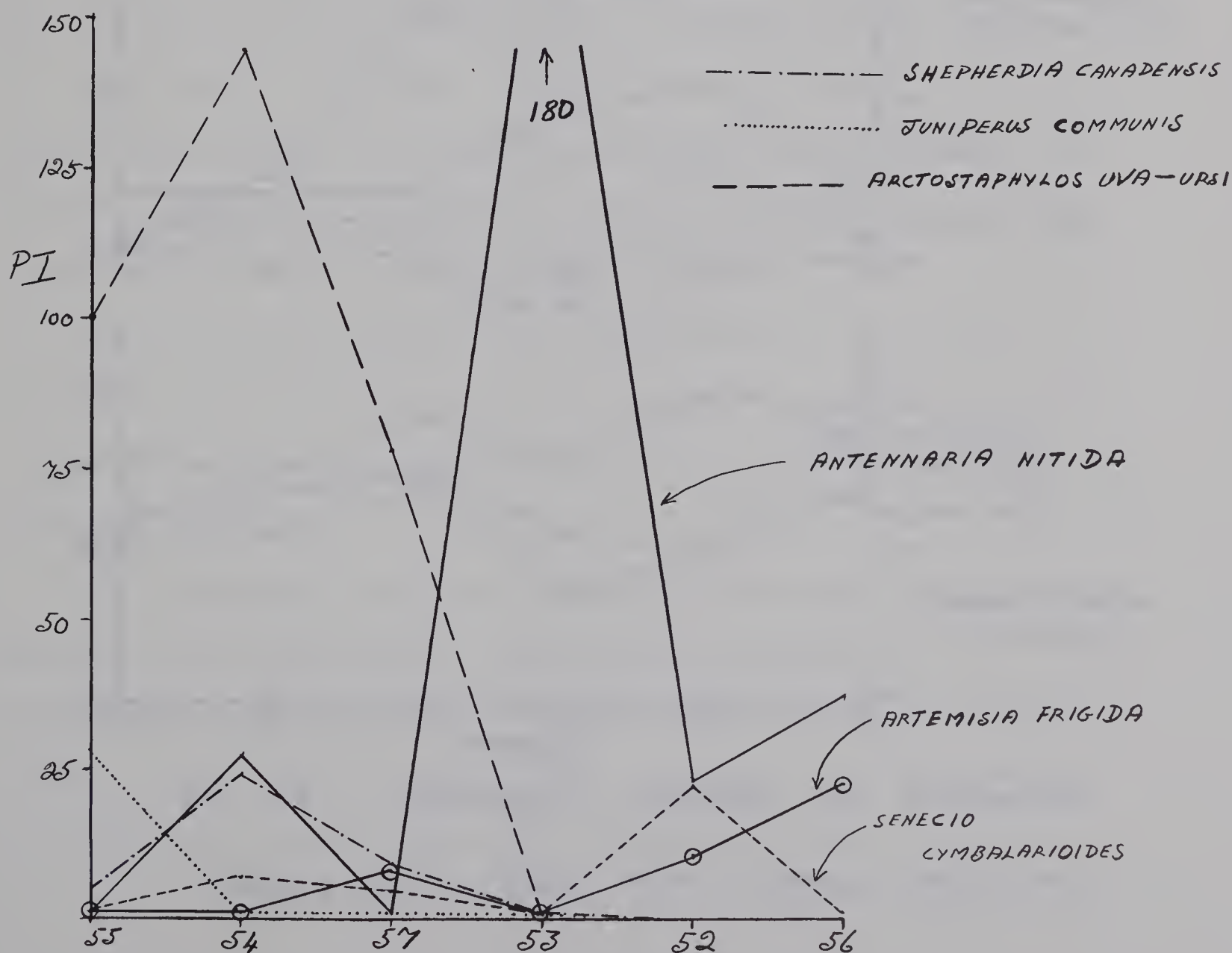
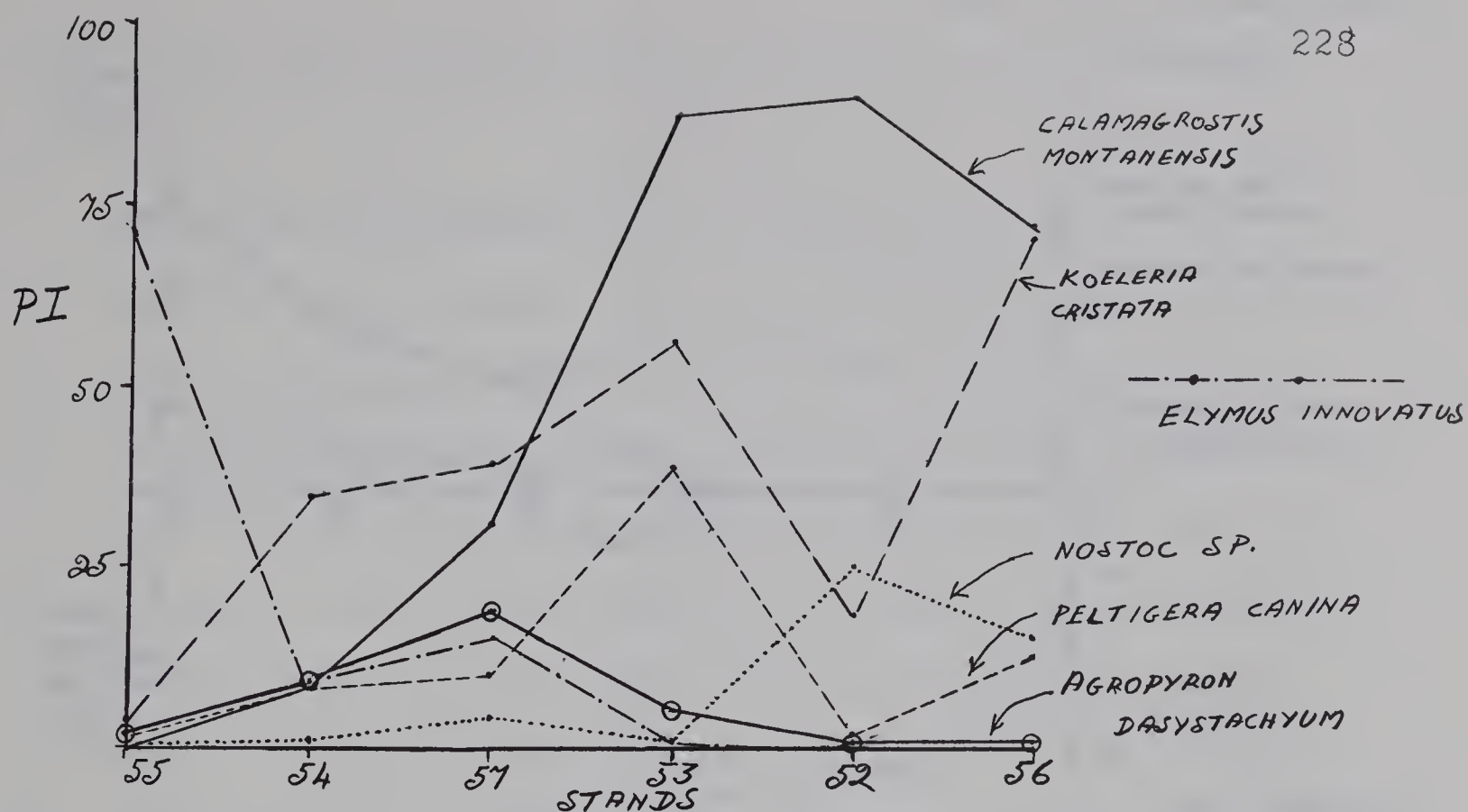


FIG. 32 PROMINENCE INDICES OF 12 SELECTED SPECIES IN THE HENRY HOUSE INTENSIVE STUDY SITE





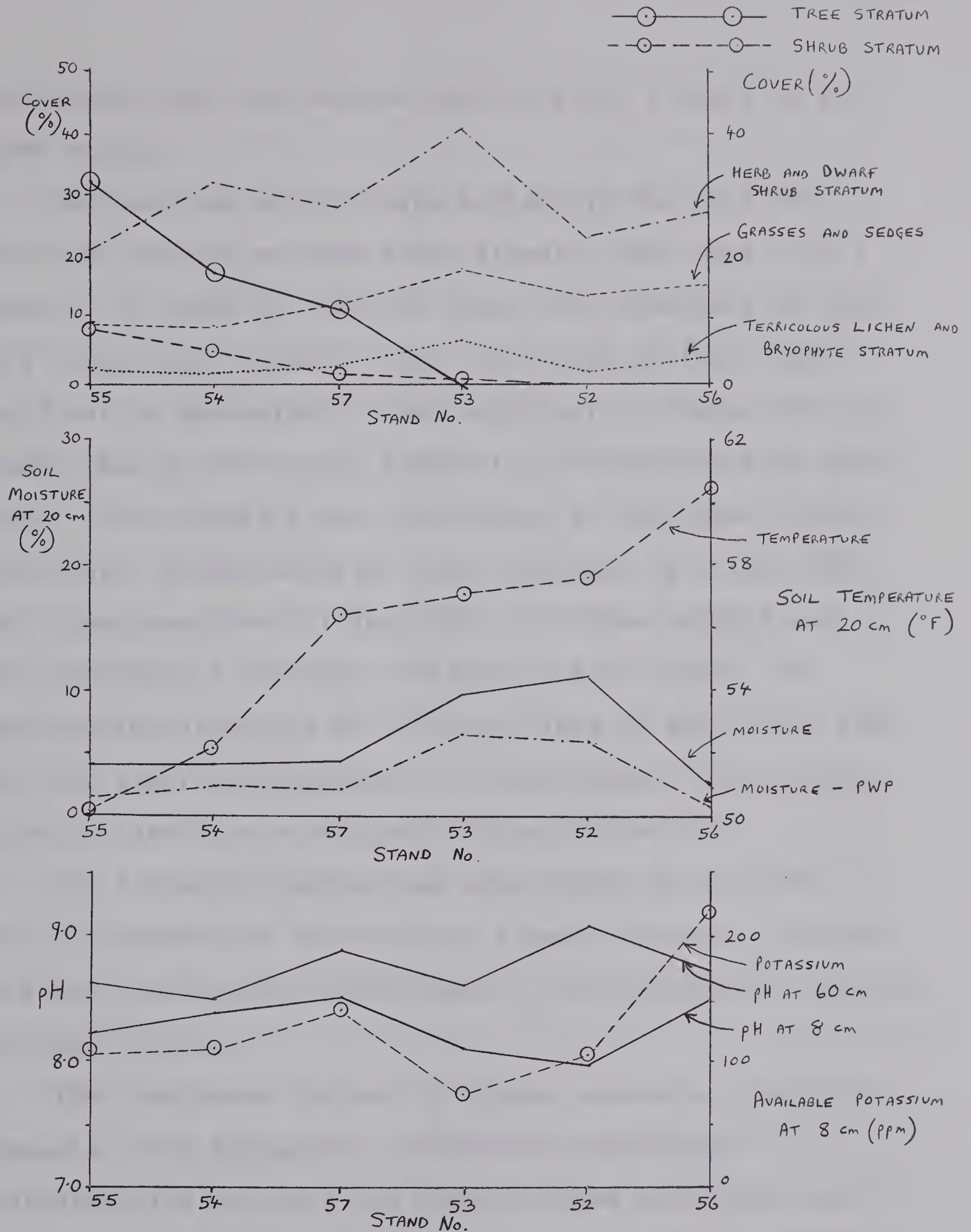


FIG. 33 VEGETATIONAL ATTRIBUTES AND ENVIRONMENTAL  
VARIABLES IN THE HENRY HOUSE INTENSIVE STUDY SITE



established that the maximum age was  $100 \pm 2$  years in all three stands.

Maximum tree height (Haga altimeter) was 45-47 ft (13-14 m) and the maximum trunk diameter (DBH tape ) 13.3 inches. In stand 57, the two trees with diameters of over 10.0 inches were rotten in the centre and so their ages could not be determined. Tree reproductive stages were not common, and in most cases seemed to be surviving with difficulty. Their density was about equal in the three stands; there were, on the average, three saplings (1-3 inch DBH), four transgressives (<1 inch DBH, >6 inches height) and five seedlings ( <6 inches height) in each stand. All reproductive stages in No. 55 were close to the forest edge. The only other tree species was white spruce (*Picea glauca*) of which there was a solitary sapling in No. 55.

The following species had mean values of 10.0 or more: *Calamagrostis montanensis*, *Elymus innovatus*, *Koeleria cristata*, *Antennaria nitida/rosea*<sup>15</sup>, *Arctostaphylos uva-ursi*; *Peltigera canina*.

The Prominence Indices of *Elymus innovatus*, *Juniperus communis*, *Rosa acicularis*, *Shepherdia canadensis*, *Arctostaphylos uva-ursi* and *Brachythecium salebrosum* were maximal at the forest end of the continuum. Covers of the tree and shrub strata were also maximal at this end (Fig. 33). These species are Dominants in the dry, lodgepole pine-Douglas fir-white spruce forests which form the major vegetation in the Athabasca River valley in Jasper National

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<sup>15</sup> See footnote, p. 59





Park. The forest understory species did not occur in the open grassland areas (Fig. 32). The grassland Dominants, however, did occur in the forests although with reduced abundance.

The Prominence Indices of the following species were maximal in the three *Koeleria-Calamagrostis* stands (52, 53 and 56): *Bromus pumpellianus*, *Calamagrostis montanensis*, *Koeleria cristata*, *Antennaria nitida/rosea*,<sup>16</sup> *Artemisia campestris*, *A. frigida*, *Astragalus tenellus*, *Erigeron caespitosus*, *Peltigera canina*, *Physcia muscigena*, *Nostoc* sp.. Angiosperm cover was maximal in stand 53 which was more mesic than the other two grassland stands. *Astragalus agrestis*, *Campanula rotundifolia*, *Antennaria nitida/rosea*<sup>17</sup>, *Peltigera canina* and the two principal mosses, *Bryum* sp. and *Ceratodon purpureus*, were maximal in stand 53 and are representative of the more abundant vegetation in slight depressions.

Only two species, *Agropyron dasystachyum* and *Carex richardsonii*, were clearly more abundant in the pine savanna stands.

Thus, nearly all the species in the Henry House intensive site can be designated either as lodgepole pine forest or *Koeleria-Calamagrostis montanensis* Grassland species and there seems to be no floristically distinct forest edge or savanna community. The two pine savanna stands

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<sup>16</sup> and <sup>17</sup> See footnote, p. 59





are mosaics of coniferous forest understory and grassland species.

The Henry House area is moderately to heavily grazed by elk, especially in winter and early spring. Pellet group counts in areas 1,800 ft<sup>2</sup> (167 m<sup>2</sup>) for stands 52-57 were, respectively, 30, 22, 39, 33, 45 and 51 for native ungulates (mostly elk, a few mule deer) and 0, 2, 3, 0, 3, 12 for horses. Thus, grazing pressure seemed to be fairly uniform over the area.

The soils were tentatively identified as Orthic Regosols or Degraded Brown Woodeds. The Ah horizon was very thin (minimum 5 cm in stands 54 and 56; maximum, 10 cm in stands 52 and 53). There was, however, no profile development in the latter two stands and the soils were classified as Regosols. Only the soil in No. 55 (forest) had a marked profile development, i.e., B horizon.

The Ah horizon contained considerable amounts of wind-deposited silt, and organic carbon content was very low (3.4% to 4.7%).

Gravel content to 90 cm was very low and exceeded 1% only in the horizons below 15-18 cm in the forest and savanna stands (Table 6, p. 123).

The soils were very consistent in texture; all were sandy loams in the top mineral horizon and all became progressively coarser with depth. There was a layer of pure sand at 15-30 cm in the grassland stands and a layer of gravelly sand at 18-36 cm in the forest and savanna



stands.

All the soils had "medium" to "high" free lime content in all horizons, except for No. 55 which had "low" values in the A and B horizons. The soils were alkaline in the Ah horizon, with pH values ranging from 7.6 in No. 55 to 8.2 in No. 56. They became progressively more alkaline with depth, with values of 8.5-9.1 in the lowest horizon tested. The grassland stands were more alkaline in all horizons than the forest and savanna stands.

The soil samples were extremely deficient in available nitrogen and phosphorus; the amounts of these two nutrients at 8 cm in all six stands were, respectively, <1ppm, and 2ppm or less. However, in Nos. 54 and 55 available phosphorus increased with depth to values of 7 and 10 ppm respectively. Values for potassium ranged from 78-223 ppm at 8 cm to 12-22 ppm at 60 cm. These figures indicate that potassium was not as limiting to plant growth as the other two nutrients measured (Pers. comm., D. Laverty). The two soils with the lowest organic content in their Ah horizons (Nos. 56 and 57) also had the highest available potassium values.

Between June 14 and June 18, 1968, the moisture contents at 20 cm of five of the six soils were a little above and the sixth (No. 52) was a little below the Permanent Wilting Percentage (Fig. 20, p. 127). In this latter stand, the Permanent Wilting Percentage of the soil was higher than in the other five stands, possible because of the higher





proportion of silt/sand in the mineral soil.

There was a trend in soil temperature at 20 cm from high values in the open grassland to low values in the pine forest soil. The soil temperature of stand 56 was 10F higher than that of stand 55.

## 5. Correlations Between Vegetation and Environment

In the preceding section, the floristic composition and vegetation structure of the Henry House intensive study area and influential edaphic and topographic variables have been described. Vegetation will now be related to environment on a quantitative basis.

By using the data from five quadrats in each of six stands, 30 observations were obtained for each of the following variables: plant cover for selected species and for shrub stratum and herb and dwarf shrub stratum; soil temperature, moisture and gravel content at 20 cm. As the terrain was almost flat, accurate topographic measurements could not be made. Therefore no topographic variables were included. Total tree cover was roughly estimated by means of five cover points (the corners and centre) in each quadrat.

Pearson correlation coefficients were calculated between variables Nos. 13-19, 23, 24, 26-28 (Table 13, p. 169), and the results presented in matrix form in Table 23. Positive or negative correlation was considered significant at the 5% probability level.







Seven multiple regression equations were computed in the same way as for the Badlands intensive site (p. 171) in order to determine which of the environmental factors are of primary importance to each of the selected species, independent of the other environmental factors measured.

Variables 13-18 and 26 in Table 13 were used as dependent variables  $Y_1 - Y_7$ , and variables 19, 23, 24, 26-28 as independent variables  $X_{19}$ ,  $X_{23}$ ,  $X_{24}$  and  $X_{26} - X_{28}$ . The same transformations on the independent variables were calculated as for the multiple regression analysis on p. 173 and were included in the equations as independent variables. Full details of the seven equations are given in Table 24.

#### (a) Interspecific and Inter-environmental Correlations

*Antennaria nitida/roæa*<sup>18</sup>, *Calamagrostis montanensis*, *Koeleria cristata* and *Peltigera canina* are positively associated with each other and form a species complex associated with the *Koeleria-Calamagrostis* Grasslands.

*Arctostaphylos uva-ursi* and *Elymus innovatus* were negatively correlated with *Calamagrostis* and *Koeleria* but were positively correlated only weakly with each other.

Soil temperature was negatively correlated with both tree cover and gravel content. The tree canopy reduces the amount of solar radiation reaching the ground surface and there are thus lower daily maximum soil temperatures. The three forest and savanna stands were the only ones with appreciable amounts of gravel in the soil profile but the

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<sup>18</sup>See footnote, p. 59





TABLE 24. HENRY HOUSE INTENSIVE STUDY SITE; MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATION BETWEEN SEVEN VEGETATIONAL ATTRIBUTES AND THE SIGNIFICANT ENVIRONMENTAL VARIABLES.

|                                                     |          |                       |             |
|-----------------------------------------------------|----------|-----------------------|-------------|
| <i>Calamagrostis montanensis</i><br>Cover ( $Y_1$ ) |          | Constant = -187.6     | TVA = 45.3% |
| <u>X</u>                                            | <u>r</u> | <u>B</u>              | <u>V</u>    |
| Log <sub>10</sub> soil temperature                  | -0.673   | 110.6                 | 45.3        |
| <i>Koeleria cristata</i><br>Cover ( $Y_2$ )         |          | Constant = 5.04       | TVA = 25.1% |
| Tree cover %                                        | -0.501   | -0.095                | 25.1        |
| <i>Arctostaphylos uva-ursi</i> Cover ( $Y_3$ )      |          | Constant = -17.6      | TVA = 71.6% |
| Tree cover %                                        | +0.687   | 0.152                 | 47.2        |
| Gravel %                                            | +0.589   | 1.61                  | 15.5        |
| Total angiosperm cover - $Y_3$                      | -0.571   | -0.203                | 2.9         |
| Log <sub>10</sub> (soil moisture - PWP)             | +0.307   | 24.35                 | 6.0         |
| <i>Elymus innovatus</i><br>Cover ( $Y_4$ )          |          | Constant = 1838.4     | TVA = 70.9% |
| Tree cover %                                        | +0.674   | 0.046*                | 45.5        |
| (Gravel %) <sup>2</sup>                             | -0.061   | -0.317                | 10.6        |
| Log <sub>10</sub> soil temperature                  | -0.607   | -1379.9               | 8.1         |
| Soil temperature                                    | -0.601   | 10.26                 | 6.7         |
| <i>Antennaria nitida/rosea</i> Cover ( $Y_5$ )      |          | Constant = -132.6     | TVA = 51.8% |
| (Soil moisture) <sup>2</sup>                        | +0.542   | 0.070                 | 29.4        |
| Soil temperature                                    | +0.329   | 1.49                  | 6.7         |
| Log <sub>10</sub> (soil moisture-PWP)               | +0.364   | 53.02                 | 15.7        |
| <i>Peltigera canina</i> Cover ( $Y_6$ )             |          | No significant terms. |             |
| Total herb and dwarf shrub Cover ( $Y_7$ )          |          | Constant = 1.15       | TVA = 32.4% |
| Soil moisture-PWP                                   | +0.569   | 2.83                  | 32.4        |

For explanation of terms and symbols, see footnotes to Table 15, p.174.



correlation between tree cover and gravel content was not quite significant at the 5% level. Soil moisture was not significantly correlated with any of the edaphic or vegetation structure variables and probably would have been more influenced by slight topographic variations.

(b) Vegetation and Environment

The multiple regression equation of total herb and dwarf shrub stratum cover contained one term (soil moisture of < 2 mm fraction-PWP) which accounted for only 32% of the variation. Thus, of the factors measured, that affecting total cover of this stratum most seems to be the available water present in the soil and not soil moisture *per se*, i.e., PWP must be taken into account.

The equation of *Koeleria cristata* cover contained only one significant term - tree cover - and accounted for only 25% of the variation. *Koeleria* is associated with open areas, where total herb and dwarf shrub covers are slightly higher. It was not correlated with any of the edaphic factors measured.

There was only one significant term in the equation of *Calamagrostis montanensis* cover.  $\log_{10}$  soil temperature accounted for 45% of the variation in the dependent variable. Tree cover and gravel content, both negatively correlated with *Calamagrostis montanensis* cover, were not represented in the equation, because of their strong correlations with soil temperature. It is notable that there were no soil





moisture terms in the equation. *Calamagrostis*, like *Koeleria cristata*, is associated with open areas where soil temperature maxima are higher than those under tree canopies.

*Antennaria nitida/rosea*<sup>19</sup> seems to be the species most sensitive to soil moisture since two of the three terms accounting for 52% of the variation were soil moisture variables. *Antennaria* seems to occur mainly on the more moist, open sites in the Henry House area.

The four terms in the equation of *Arctostaphylos uva-ursi* cover accounted for 72% of the variation. This equation was therefore the most useful of the Henry House series. *Arctostaphylos* was correlated positively with tree cover and gravel content. The equation also contained two terms which did not appear in simple correlations - total herb and dwarf shrub cover, and a soil moisture variable. *Arctostaphylos* cover is adversely affected by within-stratum competition but is promoted by tree cover and by gravelly soils with relatively high moisture contents.

The four terms in the equation of *Elymus innovatus* cover accounted for 71% of the variation and therefore indicated very well the environmental "requirements" of this species in the Henry House area. *Elymus* was positively correlated with tree cover, but, on the addition of terms 2-4 to the regression equation, this correlation lost significance. This species is primarily influenced by soil

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<sup>19</sup>See footnote, p. 59



temperature and gravel content, and in the Henry House area, occurs on soils with lower maximum temperatures, i.e., under tree canopies.

No equation was valid for *Peltigera canina* cover as neither the Partial F-test nor the regression coefficients had any significance at the 5% level.

### *Koeleria-Geum triflorum* Grasslands

#### 1. Topography, Vegetation and Soils

The four stands of *Koeleria-Geum triflorum* Grassland are in the Red Deer River valley (Nos. 21, 30, 31) and the Bow River valley (No. 33) in or close to Banff National Park and range in elevation from 4,570 ft (No. 33) to 5,720 ft (No. 31). Stands 21, 31 and 33 are small and are on very gravelly alluvium or glacial till on level ground in the bottoms of mountain valleys. Stand 30 is on a 4° W-facing slope in gently rolling grasslands on the Ya-Ha-Tinda ranch just outside the Park boundary, and was included in this study for comparison with stands 21 and 31 in the same valley.

The *Koeleria-Geum* Grasslands are in the "short grass formation" class but verge on "steppe" in the more arid areas (Fosberg, 1967). The vegetation structure of these Grasslands is very similar to that of the *Koeleria-Calamagrostis* Grasslands, in that a low grass-forb stratum and a mat-like ground cover are present in both. However,





a sparse tall forb-grass stratum was present in the most mesic stand (No. 30), and the total vascular plant cover (about 95%) was higher than in the *Koeleria-Calamagrostis* Grasslands.

The most prominent species of this grassland type are listed on p. 209. Only six species had mean cover values of 3% or more: *Helictotrichon hookeri* (6.5), *Koeleria cristata* (8.3), *Poa pratensis* (14.4, but absent from stand 31), *Antennaria nitida/rosea*<sup>20</sup> (4.1), *Geum triflorum* (16.9) and *Selaginella densa* (5.9). Since only four stands were studied, the number of Constant species was high, and included another 12 species as well as all those listed above except *Poa pratensis*. Bryophytes and lichens were not prominent, the only common species being *Abietinella abietina*, *Tortula ruralis*, *Cladonia* sp. and *Peltigera canina*.

*Koeleria-Geum triflorum* Grassland has many species typical of both the arid *Koeleria-Calamagrostis montanensis* Grasslands to which it is related at a low level of resolution (p. 109) and the more mesic *Festuca-Danthonia* Prairie (p. 110). Only *Helictotrichon*, *Geum* and *Androsace chamaejasme* occur more prominently here than elsewhere in this study, i.e., these are Differential species. Some of the prominent species in this grassland type are "increasers" and tend to occur prominently in most of those grasslands

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<sup>20</sup>See footnote, p. 59





of the three Parks which are heavily grazed by elk and/or horses, e.g., *Antennaria nitida/rosea*<sup>21</sup>, *Koeleria cristata* and *Artemisia frigida*. Thus, it is doubtful if these four stands can be considered as representing a distinct grass-land type, on the basis of a fairly high inter-stand Index of Similarity, the geographical proximity of three of the stands, and only three Differential species.

The soils of the four stands had very little in common (Table 6, p. 129). Those of stands 21, 30, 31 and 33 were tentatively identified as Orthic Regosol, Orthic Black Chernozem, Rego-Black Chernozem and Orthic Brown Wooded respectively. The depth of the Ah horizon varied from 30 cm in No. 30 to 5 cm in No. 33. The soils of stands 21, 31 and 33 were sandy-loams or loamy-sands with high gravel contents whereas No. 30 was a loam with very little gravel.

As would be expected from the soil texture, the values for Field Capacity and Permanent Wilting Percentage of the soil of stand 30 at 23 cm were much higher than in the other three stands.

On June 20, 1967, the soil moisture at 23 cm in No. 21 was 8% above Field Capacity whereas by August 5-6 soil moistures in Nos. 30 and 31 were below the Permanent Wilting Percentage by 18.1% and 0.5% respectively. On August 28, the soil moisture in No. 33 was about 4% below Permanent Wilting Percentage. It appears that, in 1967,

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<sup>21</sup>See footnote, p. 59



the soils of the *Koeleria-Geum triflorum* Grasslands began to suffer from moisture deficits about the same time as those of the *Koeleria-Calamagrostis montanensis* Grasslands and the *Festuca-Danthonia* Prairie, i.e., "some time in July".

In the A horizon, free lime was "very low" to nil and pH values were neutral to slightly alkaline. In the B and C horizons, free lime was "medium" to "high" and pH values very alkaline.

Available nitrogen in the A horizon was highest in the stand sampled in June (15 ppm) and nil in that sampled in late August. Available phosphorus was 5 ppm or less in all four stands and available potassium varied from 126 ppm to 300+ ppm. All three nutrients decreased with depth, except in stand 31 where both phosphorus and potassium increased with depth to values of 6 ppm and 192 ppm respectively in the C horizon. Thus, as in most of the other grassland soils in this study, the level of available potassium seems to be less limiting to plant growth than the levels of available nitrogen and phosphorus.

## 2. Standing Crop

Only one site of *Koeleria-Geum triflorum* Grassland was sampled for standing crop in 1968. This was a site next to stand 31 at Tyrrell Creek in the Red Deer River valley.

Estimations of standing crop were carried out as for the *Festuca-Danthonia* Prairie sites (p. 117). Unlike the





standing crop estimations made in *Festuca-Danthonia* Prairie and *Koeleria-Calamagrostis montanensis* Grasslands, the air-dry weight of graminoids was significantly higher on August 21 than on July 16 (Table 5, p. 119). Therefore, the results for the two sampling dates were not combined, and the August results were taken as being more representative of the maximum standing crop. The mean values were (kg/ha): graminoids 590 and 827, forbs 285 and 296, giving total standing crops of 875 and 1,123 for July 16 and August 21 respectively. The species which contributed most to the standing crop were *Agropyron dasystachyum*, *Carex* spp., *Koeleria cristata* and *Geum triflorum*.

These values are much lower than the standing crop estimations made in the *Festuca-Danthonia* Prairie or the Banff airstrip site, but are higher than those at the Henry House *Koeleria-Calamagrostis montanensis* Grassland site.

The Tyrrell Creek area has been heavily grazed by elk and horses in winter and early spring for many years (pellet group counts for stand 21; elk-60, horse-20, in 1,800 ft<sup>2</sup>). However, as at the Henry House site, the low standing crop value is probably due just as much to an arid gravelly soil as to heavy grazing and soil compaction.

### 3. Effects of Grazing

The pellet group counts recorded in stands 21, 30, 31 and 33 were comparatively high for this study, being respectively 60, 18, 76 and 0 in 1,800 ft<sup>2</sup> for native



ungulates, mostly elk, and 20, 38, 40 and 17 in 1,800 ft<sup>2</sup> for horses.

Stand 30 has been used for light winter grazing by Park horses, and stands 21 and 31 are in small areas that have been heavily grazed by elk and horses, mostly in winter and spring. A herd of about 250 elk in the Red Deer River valley has been active in the vicinity of stands 21 and 31 both in summer and in winter. Also, a large herd of outfitters' horses from outside the Park is moved through the valley into the Park each spring and out again in the fall. They are paddocked for a day or so each trip at Scotch Camp (No. 31). On the basis of the data available, it is difficult to assess the relative effects of elk and horses regarding the overgrazed condition of the grasslands in Nos. 21 and 31. Stand 33 has been heavily grazed by outfitters' horses in spring and early summer but apparently is not touched by elk. Ground squirrels seemed to be absent from Nos. 21, 30 and 33 but were common in No. 31.

Thus, all four of the stands in this *Koeleria-Geum triflorum* Grassland are grazed by horses, three of them heavily so at a time of year critical for growth. Stands 21, 31, and perhaps 33 can be looked on as impoverished xerophytic grasslands resulting, in part, from heavy grazing and soil compaction in a grassland type which may have been similar to but more xerophytic than that of No. 30.

The number of species decreases as grazing intensity increases in the three Red Deer River valley stands, i.e.,





from No. 31 to 21 to 30, and the Cover-abundance values of many species prominent in No. 30 decreased in Nos. 21 and 31, e.g., *Agropyron dasystachyum*, *Helictotrichon hookeri*, *Cerastium arvense*, *Oxytropis campestris* var. *gracilis* and *Potentilla gracilis*.

Soil structure is possibly another important factor causing impoverishment of the vegetation. In No. 30 there is a loam soil with a deep A horizon whereas in Nos. 21, 31 and 33 there is very gravelly, loamy-sand or sandy-loam with thin A horizons and poor moisture holding capacity.

Stand 30, dominated by *Koeleria cristata*, *Helictotrichon hookeri*, *Poa pratensis* and *Geum triflorum*, is not closely related to either *Koeleria-Calamagrostis montanensis* Grassland, *Festuca-Danthonia* Prairie or any other grassland type in this study. More extensive studies of grasslands in the same geographical area, i.e., along the eastern margins of Banff and Jasper, are needed to establish whether *Koeleria-Geum triflorum* Grassland is a distinct type or merely the result of disturbance and grazing by ungulates.

### *Stipa richardsonii* Subalpine Grassland

#### 1. Topography, Vegetation and Soils

The five stands of *Stipa richardsonii* Subalpine Grassland sampled are representative of many small, isolated areas within the *Abies-Picea-Pinus-Pseudotsuga* forests which constitute the major part of the vegetation of the subalpine





and montane zones in Banff and Jasper National Parks. These stands are at higher elevations than most others in this study, and range from 4,500 ft in Jasper (No. 50) to 5,412 ft in Banff (No. 23). They are generally in the valley bottoms on S-facing slopes of 0-5 degrees.

The *Stipa richardsonii* Subalpine Grasslands are a mixture of "short grass" and "shrub savanna" formation classes (Fosberg, 1967). Only two strata were apparent: an ill-defined, forb-grass stratum (up to 50 cm in height), and an open shrub stratum which rarely exceeded 100 cm in height (Plate 3).

The Dominant and prominent species are listed on p. 110. Species with mean cover values of 3.0% or more were: *Agropyron dasystachyum* (4.6), *Bromus pumpehianus* (4.6), *Danthonia intermedia* (5.3), *Stipa richardsonii* (20.6), *Poa pratensis* (14.7), *Arctostaphylos uva-ursi* (6.1), *Fragaria virginiana* var. *glaucæ* (7.2), *Penstemon confertus* (6.6), *Potentilla fruticosa* (6.6) and *Salix glauca* (4.6). The mean total vascular plant cover of these Grasslands was high, i.e., approximately 110%, of which 13% was due to shrub species.

There were a large number of Constant species, including *Elymus innovatus*, *Achillea millefolium*, *Anemone multifida*, *Antennaria nitida/rosea*<sup>22</sup>, *Betula glandulosa*, *Cerastium arvense*, *Gentianella amarella*, *Viola adunca*, *Abietinella abietina* and *Peltigera canina* as well as all those species listed above except *Agropyron dasystachyum*,

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<sup>22</sup>See footnote, p. 59





Plate 3.

*Stipa richardsonii* Subalpine Grassland; stand 25, Spray River, Banff National Park; shows shrub stratum of *Betula glandulosa*, *Potentilla fruticosa* and *Salix* spp., with cover (25%) unusually high for this grassland type.





*Bromus pumpellianus*, *Arctostaphylos* and *Salix glauca*. Five species were Differential to this grassland type: *Stipa richardsonii*, *Penstemon confertus*, *Betula glandulosa*, *Potentilla fruticosa* and *Salix glauca*.

A striking feature of these Grasslands was the prominence of a shrub stratum which was better developed here than elsewhere in this study, except for the *Elymus innovatus* Subalpine Shrub Savanna. Stand 22 was atypical because of its extremely high cover of *Poa pratensis*, low species diversity (19) and the absence of shrubs from the immediate stand site. There were, in the *Stipa richardsonii* Subalpine Grasslands, a number of species (e.g., *Elymus innovatus*, *Arctostaphylos uva-ursi*, *Fragaria virginiana* var. *glauca*, *Abietinella abietina*) which are more typical of xerophytic coniferous forest such as the nearby *Abies-Picea-Pinus-Pseudotsuga* forest.

Bryophytes and non-crustose lichens were a little more prominent in these Grasslands than in the other grassland types, the mosses being especially prominent in the shade of the shrubs. The most common bryophytes and lichens were *Abietinella abietina*, *Brachythecium salebrosum*, *Dicranum fuscescens*, *Tortula ruralis*; *Cetraria ericetorum*, *Cladonia* spp. and *Peltigera canina*. *Dicranum fuscescens* was not found elsewhere in this study.

These Grasslands were not closely related to any of the other grassland types in this study and there are enough Differential species to warrant the recognition of the *Stipa*



*richardsonii* Subalpine Grassland as a distinct grassland type although it is of limited area, scattered distribution and variable composition.

The soils of the *Stipa richardsonii* Subalpine Grasslands were highly variable, and no two soil profiles were alike (Table 6, p. 123). Stands 22, 34 and 50 were tentatively identified as Orthic Black Chernozem, Orthic Regosol and Degraded Brown Wooded respectively. Stands 23 and 25 were not identified as their descriptions did not seem to fit into the soil classification system used (National Soil Survey Committee, 1968). However, both soils were probably Regosols, because of their seemingly undeveloped profiles. Stands 25 and 34 had two buried profiles each, at depths below 30 cm. This indicated periodic flooding.

The gravel content of the soil profiles varied greatly. Stands 22, 23 and 25 had respectively 8%, 80% and 7% gravel in their profiles to 90 cm, the amounts increasing with depth. Stand 34 had no gravel and stand 50 had a layer of coarse gravel below 36 cm.

The < 2mm fractions were all sandy-loams or sands, the texture becoming less coarse with depth in Nos. 22, 25 and 34. Stand 50 had a clay-loam horizon at 30-36 cm.

Since the profile types varied widely, the Permanent Wilting Percentage and Field Capacity values at 23 cm also varied widely, the former varying from 1.9% to 16.8% and the latter varying from 6.2% to 33.2%.

Although the five soil profiles were of widely varied





types, most of the soils of the *Stipa richardsonii* Subalpine Grasslands seemed to develop soil moisture deficits in the summer of 1967 to as large an extent as those of the grassland types previously described. On June 21, 1967, the soil moisture at 23 cm in No. 22 seemed to be well above Field Capacity. However, the validity of this reading is doubtful as the transition from Ah to B horizon was at about 23 cm and there was a correspondingly large change in Field Capacity at this depth. On July 9, the soil moisture in No. 23 was below the Permanent Wilting Percentage. Stand 23 had a very gravelly, xeric soil profile and had the lowest total cover in this grassland type (82%). The soil moistures of Nos. 25, 34 and 50, measured on July 9, August 29 and August 19 respectively, were all between Field Capacity and Permanent Wilting Percentage. These soils had 9.3%, 2.9% and 3.4% available water present.

Although no precipitation and temperature data are available for high elevations in Jasper or Banff National Parks, it is to be expected that grassland stands at higher elevations would receive more precipitation and have cooler daytime temperatures than those at lower elevations, and would therefore have lower evapotranspiration: precipitation ratios.

In all the soils, free lime was "low" to nil in the A horizons and "medium" to "high" in all lower horizons, except in stand 25 where free lime was "medium" in the Ah horizon, "high" at intermediate depths but only a trace below 56 cm.





The pH values in all horizons below the A horizon were alkaline (7.8-8.3), but those in the A horizon varied from alkaline in No.22 to near neutral in Nos. 23, 25 and 34 to acid in No. . 50 (6.0).

Available nitrogen varied from 9.5 ppm to nil in the A horizon on the date of sampling and decreased to 1 ppm or less in lower horizons except in No. 23 where available nitrogen was 2-2.5 ppm throughout the profile. Available phosphorus varied from 7.5 ppm to 2.5 ppm in the A horizon and decreased to 1 ppm or less in lower horizons except in stand 50. Available potassium was extremely variable and ranged from 234 ppm to 89 ppm in the A horizon and from 75 ppm to 29 ppm in the lower horizons. Available phosphorus and potassium increased slightly in the lowest horizon in No. 50 (below 36 cm) to 5 ppm and 65 ppm respectively.

Thus, the soils of the *Stipa richardsonii* Subalpine Grasslands are very variable and, on the basis of available data, no generalisations can be made regarding their distinctness from the soils of the other grassland types. It seems probable that other environmental factors, such as soil temperature régime and annual snowfall, govern the occurrence of *Stipa richardsonii* Subalpine Grasslands.

## 2. Standing Crop

One area of *Stipa richardsonii* Subalpine Grasslands was sampled for standing crop in 1968. This was a site immediately S of stand 22 in Hillsdale Meadows, Banff National Park.



Estimations of standing crop were made as for the *Festuca-Danthonia* Prairie sites (p. 117). The air-dry weight of graminoids but not that of forbs from five cones sampled on August 22 was significantly higher at the 10% level than that from those sampled on July 15 (Table 5, p. 119). The results were not, therefore, combined, and the August results were taken as more representative of the maximum standing crop. The mean values (kg/ha) were: graminoids 1,533 and 2,279, and forbs 281 and 299, giving total standing crops of 1,814 and 2,578 for July 15 and August 22 respectively. The species which contributed most to the standing crop were the graminoids *Agropyron trachycaulum* var. *unilaterale*, *Poa pratensis*, *Stipa richardsonii*, *Carex* spp. and, to a lesser extent, the forbs *Fragaria virginiana* var. *glauca*, *Potentilla gracilis* and *Senecio indecorus*. The sporadic distribution of large bunch grasses such as *Stipa richardsonii*, *Festuca scabrella* and *Agropyron trachycaulum* var. *unilaterale* was the main reason for the large variation in standing crop value from cone to cone. On August 22, the crop of graminoids varied from 1,488 to 3,182 kg/ha and the total crop varied from 1,877 to 3,289 kg/ha.

These standing crop values for graminoids were much higher than those in any of the other sites except some of the Hay Meadow cones at Waterton. The standing crop values of forbs were lower than those in any other site except the heavily-grazed Henry House and Tyrrell Creek sites. The crop of graminoids at Hillsdale Meadow was high because the





site is very little grazed because the cones were in the most mesic part of the meadow where the soil is rich, deep and chernozemic. The Hillsdale exclosure plot (see next Section) and stand 22 were both higher up the slope of Hillsdale Meadow and on less mesic sites, as the crop values from inside the exclosure show (p. 255). The Hillsdale Meadow site cannot be regarded as typical of the *Stipa richardsonii* Subalpine Grasslands with respect to standing crop; stands 23 and 50, at any rate, have much smaller crops, due to much more xeric soils.

### 3. Effects of Grazing

The pellet group counts were among the lowest recorded in this study: 0, 0, 10, 9 and 4 in 1,800 ft<sup>2</sup> for native ungulates (mostly elk), and 0, 1, 5, 0 and 10 in 1,800 ft<sup>2</sup> for horses in stands 22, 23, 25, 34 and 50 respectively. Thus, none of the five sites has been heavily grazed recently. Elk appear to browse and graze occasionally in stands 25, 50 and 34 while mule deer and moose also graze and browse in the latter stand, probably mostly during winter and spring. Horses passing on the nearby riding trails may graze Nos. 25 and 50 occasionally.

It appears that grazing or browsing is not the major factor in the maintenance of these small, isolated Grasslands. However, this conclusion is based on limited evidence.

Four exclosures were set up by Canadian Wildlife Service biologists in Banff National Park in the spring of



1944 in order to study the effects of excluding ungulates from several vegetation types. One enclosure (30 ft x 50 ft = 9 m x 15 m) at Hillsdale Meadows is in *Stipa richardsonii* Subalpine Grassland immediately N of stand 22 and about 300 ft N of the Hillsdale Meadow standing crop site. This enclosure was sampled in July, 1968 in the same way as the six already discussed (p. 148 and p. 216).

There were 9 elk pellet groups in 1,000 ft<sup>2</sup> just outside the enclosure, indicating light grazing by elk, probably during winter and spring.

There were significantly higher cover values of *Agropyron trachycaulum* var. *unilaterale*, total graminoids and total angiosperms outside the enclosure plot (Table 25). There was also slightly greater cover of *Poa pratensis* and of *Stipa richardsonii* outside and of *Penstemon confertus* inside the plot but the results were not significant at the 5% probability level. There appeared to be far more litter inside the enclosure but this difference was not verified by cover point data.

*Tortula ruralis*, the only common moss inside the enclosure, was absent in the area immediately outside the enclosure.

Culms of the most prominent grass, *Poa pratensis*, were 8 cm taller inside the enclosure (significant at 5%).

The total standing crop inside the enclosure was 1,548 kg/ha (1,467 kg/ha of graminoids and 81 kg/ha of forbs). This crop value is considerably less than that recorded from



TABLE 25. HILLSDALE MEADOW EXCLOSURE PLOT.

|                                                                                  | Mean<br>Inside <sup>1</sup> | Mean<br>Outside <sup>1</sup> | t        |
|----------------------------------------------------------------------------------|-----------------------------|------------------------------|----------|
| Litter Cover, %                                                                  | 79.8                        | 88.0                         | 3.0000*  |
| Angiosperm Cover, %                                                              | 57.5                        | 80.0                         | 4.6169** |
| Graminoid Cover, %                                                               | 48.8                        | 73.3                         | 3.7380** |
| <i>Agropyron trachycaulum</i> var.<br><i>unilaterale</i> Cover, %                | 5.3                         | 15.0                         | 4.2637** |
| <i>Poa pratensis</i> Cover, %                                                    | 24.8                        | 35.5                         | 1.6366   |
| <i>Stipa richardsonii</i> Cover, %                                               | 9.5                         | 13.8                         | 1.0166   |
| <i>Penstemon confertus</i> Cover, %                                              | 6.8                         | 0.5                          | 1.4598   |
| <i>Tortula ruralis</i> Cover, %                                                  | 7.3                         | 0.0                          | --       |
| <i>Poa pratensis</i> , height <sup>3</sup>                                       | 13.3                        | 10.3                         | 3.6662** |
| Angiosperm standing crop, kg/ha                                                  | 1548                        | 1689                         | 0.5717   |
| Graminoid standing crop, kg/ha                                                   | 1467                        | 1592                         | 0.4507   |
| <i>Agropyron trachycaulum</i> var.<br><i>unilaterale</i> standing crop,<br>kg/ha | 43                          | 206                          | 7.9621** |
| <i>Poa pratensis</i> standing crop,<br>kg/ha                                     | 1103                        | 879                          | 0.6689   |
| <i>Stipa columbiana</i> standing crop,<br>kg/ha                                  | 86                          | 216                          | 1.7567   |
| <i>Stipa richardsonii</i> standing<br>crop, kg/ha                                | 223                         | 292                          | 0.3643   |
| Soil temperature at 15 cm, °F.                                                   | 54.0                        | 54.0                         | 0.0000   |
| Soil moisture at 2-5 cm, %.                                                      | 43.5                        | 43.7                         | 0.0352   |
| Soil moisture at 15-20 cm, %.                                                    | 32.8                        | 28.0                         | 0.8054   |
| Organic carbon at 2-5 cm, %.                                                     | 11.1                        | 12.0                         | 0.5516   |
| Organic carbon at 15-20 cm, %.                                                   | 3.4                         | 5.1                          | 1.2874   |

Footnotes: <sup>1</sup> - see Table 8, p.149.<sup>2</sup> - see Table 8, p.149.<sup>3</sup> - see Table 19, p.217.





the Hillsdale Meadow site selected for standing crop estimates (p. 253). The latter area was 300 ft lower in elevation and was more mesic. Only *Agropyron trachycaulum* var. *unilaterale* had significantly more crop outside the enclosure; the crop of *Poa pratensis* was greater inside and that of *Stipa columbiana* greater outside but these results were not statistically significant.

Thus, protection from light grazing by native ungulates has decreased the cover of the Dominant grasses and has reduced the standing crop of the *Agropyron*. . It seems, therefore, that light grazing has been beneficial to the grassland at this site. The apparently excessive build-up of litter (*i.e.* "carry-over") inside the enclosure might have been confirmed had estimations of the standing crop of litter been made.

The soil profiles inside and outside the enclosure were nearly identical. The Ah horizon inside the enclosure was about 2 cm thinner than that outside. There were no significant differences in any of the soil characteristics measured.



*Elymus innovatus* Subalpine

Shrub Savanna

Stands 24 and 26 are representative of a number of isolated, grassy areas at relatively high elevations in the subalpine spruce-fir zone in Banff and Jasper National Parks. These areas are generally on fairly steep, S-facing slopes and are probably kept clear of forest by frequent snow slides, occasional rock-falls and perhaps also because the habitat is more xeric than is normal for that elevation. Nos. 24 and 26 were at Redearth and Healy creeks in Banff Park at mean elevations of 5,533 ft and 5,386 ft on SE-facing slopes of 12 and 26 degrees respectively.

The two stands had very distinctive species compositions and low Index of Similarity values ( $<30$ ) with all the other stands. Their closest affinities were with stands 23 and 25 in the *Stipa richardsonii* Subalpine Grasslands and with stand 55, the pine forest stand in the Henry House intensive area. The mean Index of Similarity between 24 and 26, and 23 and 25 was 23.5; the mean value between 24 and 26, each with 55, was 27.0. The similarity between stands 24 and 26 and 55 was due to the prominence of coniferous forest understory species such as *Elymus innovatus*, *Arctostaphylos uva-ursi* and *Rosa acicularis*.

There were only two strata apparent in these Grasslands: a well-defined, open, shrub stratum, and a nearly-closed, forb-grass stratum. These Grasslands, because of the former





stratum, are in the "shrub savanna formation" class (Fosberg, 1967). Both the strata were similar in height and cover to those in the *Stipa richardsonii* Subalpine Grasslands, except that the total shrub species cover was greater (approximately 30%).

Species with mean cover values of 3.0% or more (Dominants) were: *Elymus innovatus* (41.3); *Amelanchier alnifolia* (5.3), *Arctostaphylos uva-ursi* (3.0), *Fragaria virginiana* var. *glauca* (5.3), *Galium boreale* (5.1), *Hedysarum sulphurescens* (10.3), *Rosa acicularis* (15.0) and *Rubus strigosus* (5.0). Important Differential species were *Elymus*, *Rosa* and *Rubus*. *Rubus* was found only in stand 24 in this study. *Hackelia floribunda* was prominent (Cover-abundance  $\geq 1$ ) in stand 24 and the following species were prominent in stand 26: *Agropyron dasystachyum*, *Bromus pumpellianus*, *Poa pratensis*; *Aster ciliolatus*, *Aster conspicuus*, *Juniperus communis*, *Lonicera dioica* var. *glaucescens*, *Prunus pensylvanica*, *Senecio indecorus*, *Symphoricarpos albus* and *Vicia americana*. Many of these species were uncommon in the other stands in this study, especially *Aster* spp., *Hackelia*, *Lonicera* and *Prunus*, and can thus also be considered Differentials. It is notable that *Elymus innovatus*, the only grass among the Dominants, was by far the most abundant of the Dominants. Three of the eight Dominants were shrubs.

Shrubs have an important role in *Elymus innovatus* Subalpine Shrub Savanna and the following seven species formed an intermittent but distinct stratum above the herb



and dwarf shrub stratum: *Amelanchier alnifolia*, *Rosa acicularis*, *Rubus strigosus*, *Juniperus communis*, *Lonicera dioica* var. *glaucescens*, *Prunus pensylvanica* and *Symphoricarpos albus*.

The prominence of shrubs and forest understory species suggests that the *Elymus innovatus* Subalpine Shrub Savanna should be considered as a distinct vegetation type associated with factors which prevent or arrest the development of tree and tall shrub strata.

Lichens were absent and the only mosses found were *Brachythecium salebrosum* and *Tortula ruralis*.

Pellet group counts for stands 24 and 26 were 20 and 10 in 1,800 ft<sup>2</sup> (167 m<sup>2</sup>) for native ungulates (mostly elk), and 0 and 1 in 1,800 ft<sup>2</sup> for horses. These two stands have been only moderately grazed in recent years.

The soils of both stands were composed mostly of large, angular rocks and coarse gravel, and resembled stabilised rock-falls. There were no discernible horizons; the A horizon was dispersed among the rocks and gravel to at least 30 cm depth, but was somewhat more concentrated in the thick turf at the surface. The <2 mm fraction was only 21% and 38% of the whole in stands 24 and 26 and was sandy-loam in each case.

Free lime was absent from the surface horizon but increased to "medium"—"high" further down the profile. The pH values at 8 cm in stands 24 and 26 were 7.2 and 7.4, and increased with depth (7.8 and 8.1). Available nitrogen varied





from 2 ppm-6 ppm but showed no trend in the profile. Available phosphorus was 15.5 ppm and 9.5 ppm at 8 cm in Nos. 24 and 26 respectively and, with increasing depth, decreased to 2 ppm and nil. Available potassium varied from 78 ppm to 272 ppm and did not decrease much with increasing depth.

The soil moisture readings at 23 cm on July 8-10, 1967 in stands 24 and 26 were 21.6% and 18.6%. These values were both considerably below the Permanent Wilting Percentages (43.0% and 30.4%) and indicated a very high soil moisture stress at 23 cm depth.

#### *Poa-Hordeum jubatum* Grasslands

Stands 40, 41 and 46 were chosen for sampling as representative of the "Buffalo prairie" grasslands S-E of Jasper townsite. These grasslands form flat, narrow strips on the alluvium along the bottoms of narrow, generally steep-sided valleys. Cluster analysis showed that stand 41 had affinities with stands 40 and 46 but was a satellite of the *Koeleria-Calamagrostis montanensis* Grasslands.

Stands 40 and 46 had very distinctive species compositions and had very low Index of Similarity values (<30) with all the other stands in this study except No. 41, the third stand in the Buffalo prairie area, (Index of Similarity = 35.3 with No. 40 and 36.8 with No. 46), and No. 22, a *Stipa richardsonii* Subalpine Grassland stand, in Banff National Park (Index of Similarity of No. 22 with No. 40 = 36.6).





Species with mean cover values of 3% or more (Dominants) were: *Agropyron trachycaulum* var. *unilaterale* (6.5), *Hordeum jubatum* (11.5), *Poa palustris* (18.8), *Poa pratensis* (15.0), *Carex eleocharis* (5.3); *Potentilla anserina* (20.0) and *Potentilla pensylvanica* (6.5). Species Differential to these *Poa-Hordeum jubatum* Grasslands were *Poa palustris*, *Hordeum jubatum* and *Potentilla anserina*, the last two of which were found only in this grassland type.

There was no stratification apparent, and shrubs, although generally prominent in the Buffalo Prairie valleys, were uncommon and heavily browsed in the sampled stands.

The pellet group counts in stands 40 and 46 respectively were 27 and 18 in 1,800 ft<sup>2</sup> (167 m<sup>2</sup>) for native ungulates and 3 and 4 in 1,800 ft<sup>2</sup> for horses. The counts indicated moderate grazing by elk and lighter grazing by mule deer, bighorn sheep and horses. However, the species which increased due to grazing in the *Koeleria-Calamagrostis montanensis* Grasslands (see p. 223) were uncommon or absent from these two stands.

There were no common lichens, but the mosses *Bryum* sp., *Tortula ruralis* and, in No. 40 especially *Ceratodon purpureus*, were prominent. Several charred tree stumps in No. 40 indicated a fire history and suggested that this site was formerly wooded, if not forested.

The distinctness of this grassland type and its lack of similarity to any other in this study could be due to (a) the presence of a heavy clay soil (b) the possibility



of occasional spring flooding because of the low-lying topography.

The soils of stands 40 and 46 were tentatively identified as Rego-Black Chernozem and Orthic Regosol respectively, with Ah horizons 10 and 5 cm thick and little or no B horizon development. There was no gravel in the profiles and the soil textures were, in No. 40, clay changing to heavy clay at 46 cm and in No. 46 clay-loam. The surface of stand 46 was slightly undulating, the microrelief being about 1 ft. The higher areas had beds of sand close to the surface below the clay-loam and were sparsely covered with vegetation, the prominent species being *Carex eleocharis* and *Potentilla pensylvanica*. The other Dominants produced a much more abundant vegetation in the lower areas where no sand was detected to 90 cm in the main soil pit.

In 1967, the soil moisture at 23 cm was 15.1% on July 16 in No. 40 and 8.8% on August 10 in No. 46. These values were respectively 2.3% above and 3.8% below the Permanent Wilting Percentages. These results indicate a shortage of available water by August, 1967.

Free lime was nil or a trace in the Ah horizon. Both profiles were acid. The pH values in the Ah horizons were 5.5 (No.40) and 6.2 (No. 46), increasing only slightly with depth to 5.9 and 6.3 respectively.

Available nitrogen was 1 ppm or less in the Ah horizons in both stands and, with increasing depth, dropped to nil in No. 46 but increased to 3.5 ppm in No. 40. Available





phosphorus and potassium in the Ah horizon were 3.5 ppm and 161 ppm in No. 40 and 5 ppm and 115 ppm in No. 46. The amounts of these nutrients decreased with depth. The values found for the three nutrients are roughly equivalent to those found in the *Koeleria-Calamagrostis montanensis* Grasslands, currently the prevalent grassland type in Jasper National Park.

To one side of stand 40, there was a completely bare patch of soil about 600 ft<sup>2</sup> in area (55 m<sup>2</sup>). This was probably a discharge area of ground water from the nearby steep valley side. *Hordeum jubatum* and *Potentilla anserina* were far more abundant close to this patch than in the stand itself. The soil of this patch was a heavy, very acid clay (pH 4.6), with a much higher conductivity than the other soils in this study (1.8 mmhos; "normal" about 0.2-0.5 mmhos). The soil also had an unusually high available nitrogen content (40+ ppm). Available phosphorus and potassium were considered normal (2.5 ppm and 141 ppm respectively). Sodium (42 ppm) and sulphate ("low") were also a little higher than usual.

Since these two stands have distinctive vegetation and soils, they should be considered representative of a distinct grassland type, *Poa-Hordeum jubatum* Grassland, of limited occurrence in the study area, due to local, mainly edaphic features, e.g., acid clay soil.



Correlations Between Vegetation and Environment  
in Banff and Jasper National Parks

The vegetation, soils and topography of stands of the major grassland types in Banff and Jasper National Parks have been described in preceding sections, but little attempt has been made to investigate possible correlations between vegetation and environment. The data obtained from the 31 stands (Nos. 21-51) in Banff and Jasper National Parks in the summer of 1967 are suitable for such investigations. Data from stands 1-20 in Waterton Lakes National Park were not included because the vegetation and environment in this group of stands differed greatly from those of stands 21-51. Data from stands 52-71 were not included because these stands were sampled a year later than stands 21-51 in 1968, and under very different weather conditions, as described on p. 46 and following.

Only six species in the 31 stands had high enough Presence values (80% or almost 80%) as well as adequate Cover-abundance values ( $>0.5$ ) to warrant their inclusion in quantitative correlation calculations. Pearson correlation coefficients ("r") were calculated between the Cover-abundance scale values of these six species to assess their degree of association, and between these Cover-abundance values and all the environmental factors for which a stand value was available (Table 26). The coefficients are



presented in matrix form in Table 27. Much of the soil data has been condensed to one value for each profile, by using either the weighted mean of the mineral horizons or the value at the depth considered most meaningful.

Multiple regression analysis was carried out as for the Badlands intensive area in an attempt to determine which of the environmental factors measured are of primary importance to the species, independent of the other environmental factors measured. Multiple regression detects any significant correlations between the species used as dependent variables and the environmental variables. At a simple correlation level, such correlations are obscured by inter-environmental correlations. The six selected species and total angiosperm cover were used as dependent variables, and variables 1-23 in Table 26 as independent variables. The seven equations are given in Table 28. The only transformation used was " $\sqrt{\text{Gravel\%}}$ " instead of "gravel%" as the former was found in previous sections to be the more useful in the regression equations.

## 1. Interspecific Association

*Koeleria cristata*, *Antennaria nitida/rosea*<sup>2 3</sup>, *Artemisia frigida* and *Astragalus striatus* were positively correlated with each other (Table 27). These four species were all associated with the xerophytic *Koeleria-Calamagrostis*

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<sup>2 3</sup> See footnote, p. 59





TABLE 26. VEGETATIONAL AND ENVIRONMENTAL VARIABLES USED IN SIMPLE CORRELATIONS AND IN MULTIPLE REGRESSION ANALYSIS: STANDS 21-51 (1967) BANFF AND JASPER NATIONAL PARKS.

1. Grazing intensity of native ungulates (pellet groups in 1,800 ft<sup>2</sup> = 167m<sup>2</sup>).
2. Grazing intensity of horses (pellet groups in 1,800 ft<sup>2</sup> = 167m<sup>2</sup>).
3. Elevation corrected for latitude, in ft.
4. Slope aspect.<sup>1</sup>
5. Slope angle, in degrees.
6. Available nitrogen at 8 cm, ppm.
7. Available phosphorus at 8 cm, ppm.
8. Available potassium at 8 cm, ppm.
9. pH at 8 cm.
10. Free lime at 8 cm.<sup>2</sup>
11. Free lime at 60 cm.<sup>2</sup>
12. Soil moisture at 23 cm, % at date of sampling.
13. Soil moisture at 23 cm, <2 mm basis, % at date of sampling.
14. Field capacity, %, at 23 cm, (1/3 atm.).
15. Permanent wilting percentage at 23 cm, (15 atm.).
16. Available water % at 23 cm.
17. Soil moisture at 23 cm, <2 mm basis - PWP, %, at date of sampling.
18. Sand, %, weighted mean to 90 cm.
19. Silt, %, weighted mean to 90 cm.
20. Clay, %, weighted mean to 90 cm.
21. Date of sampling.<sup>3</sup>
22. Total Angiosperm cover, %.<sup>4, 5</sup>
23. Gravel, %.
24. *Agropyron dasystachyum* Cover, %.<sup>4</sup>
25. *Koeleria cristata* Cover %.<sup>4</sup>
26. *Poa pratensis* Cover, %.<sup>4</sup>
27. *Antennaria nitida/rosea* Cover %.<sup>4</sup>
28. *Astragalus striatus* Cover, %.<sup>4</sup>
29. *Artemisia frigida* Cover, %.<sup>4</sup>

- Footnotes:
- <sup>1</sup> - Scale: South = 1, SE and SW = 2, East, West and flat = 3, NE and NW = 4, North = 5.
  - <sup>2</sup> - Scale: Very high = 5, high = 4, medium = 3, low = 2, trace = 1, nil = 0.
  - <sup>3</sup> - Scale: June 1, 1967 to August 31, 1967 = 1-92.
  - <sup>4</sup> - Calculated from the Cover-abundance values:  
P, +, 1, 2, 3, 4, 5, 6, = 0.1, 0.5, 3.0, 10.0  
20.0, 37.5, 62.5 and 87.5 % respectively.
  - <sup>5</sup> - For correlations between total angiosperm cover and the cover of single species (variables nos. 24-29) the value "total angiosperm cover - species cover" was used.



TABLE 27. CORRELATIONS BETWEEN THE MAJOR VEGETATIONAL ATTRIBUTES AND

ENVIRONMENTAL VARIABLES; STANDS 21-51.

Pearson correlation coefficients between pairs of variables listed in Table 26 attaining a 5% level of significance ( $r = 0.3494$ ) indicated as "+" or "-", 1% level ( $r = 0.4487$ ) as "++" or "--".

| Variables | 29 | 28 | 27 | 26 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9  | 8  | 7  | 6  | 5  | 4 | 3 | 2  |
|-----------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|----|
| 1         | ++ | +  | ++ | -  | ++ | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | -  | .  | ++ | ++ | ++ | -  | -  | .  | . | . | -  |
| 2         | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | ++ | . | . | ++ |
| 3         | -- | .  | -- | .  | -- | .  | ++ | .  | .  | .  | .  | .  | ++ | .  | .  | .  | ++ | .  | .  | .  | .  | .  | .  | ++ | ++ | + | . | .  |
| 4         | .  | +  | +  | .  | +  | .  | .  | .  | ++ | .  | .  | .  | .  | .  | -- | .  | .  | -- | .  | +  | .  | .  | .  | .  | .  | . | . | .  |
| 5         | .  | .  | -  | .  | .  | .  | .  | .  | .  | .  | +  | .  | .  | .  | ++ | +  | +  | .  | -  | .  | .  | .  | ++ | .  | .  | . | . | .  |
| 6         | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | +  | .  | .  | .  | +  | ++ | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 7         | -  | .  | -  | .  | -- | .  | +  | .  | .  | .  | .  | .  | ++ | .  | ++ | ++ | ++ | +  | -  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 8         | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 9         | ++ | +  | ++ | .  | ++ | .  | .  | .  | .  | -- | .  | +  | .  | -- | .  | -  | .  | .  | .  | ++ | ++ | -- | -- | .  | .  | . | . | .  |
| 10        | ++ | ++ | ++ | .  | ++ | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | -  | .  | .  | .  | ++ | ++ | .  | .  | .  | .  | . | . | .  |
| 11        | .  | +  | .  | .  | .  | .  | .  | .  | .  | -- | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 12        | .  | -- | -- | ++ | -- | .  | .  | .  | -  | .  | .  | .  | ++ | .  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 13        | .  | -  | -  | .  | -  | .  | +  | .  | -  | .  | .  | .  | ++ | .  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 14        | .  | -  | .  | .  | -  | .  | .  | +  | .  | +  | .  | .  | ++ | .  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 15        | .  | -  | .  | .  | .  | .  | .  | .  | .  | .  | +  | -- | .  | .  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 16        | .  | .  | .  | .  | .  | .  | .  | .  | .  | ++ | .  | .  | .  | +  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 17        | .  | .  | .  | .  | -  | .  | ++ | .  | -- | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 18        | .  | .  | +  | .  | .  | .  | ++ | .  | .  | .  | .  | .  | ++ | .  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 19        | .  | .  | -  | .  | .  | .  | .  | .  | .  | .  | +  | .  | ++ | .  | .  | ++ | ++ | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 20        | .  | .  | .  | .  | .  | .  | .  | .  | .  | ++ | .  | -- | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 21        | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 22        | -  | .  | -  | .  | -- | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 23        | -  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 24        | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 25        | ++ | .  | ++ | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 26        | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 27        | .  | ++ | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 28        | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |
| 29        | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | .  | . | . | .  |





TABLE 28. MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATIONS BETWEEN SEVEN VEGETATIONAL ATTRIBUTES AND THE SIGNIFICANT ENVIRONMENTAL VARIABLES; STANDS 21-51 (1967); BANFF AND JASPER NATIONAL PARKS.

|                                                           |          |                   |             |
|-----------------------------------------------------------|----------|-------------------|-------------|
| <i>Agropyron dasystachyum</i><br>Cover ( $Y_1$ )          |          | Constant = -1.180 | TVA = 30.7% |
| <u>X</u>                                                  | <u>r</u> | <u>B</u>          | <u>V</u>    |
| Slope angle                                               | +0.302   | 0.067             | 9.1         |
| Free lime at 60 cm                                        | +0.165   | 0.342             | 9.7         |
| Available water at<br>23 cm, %.                           | +0.159   | 0.045             | 11.9        |
| <i>Koeleria cristata</i><br>Cover ( $Y_2$ )               |          | Constant = 4.161  | TVA = 78.8% |
| Grazing intensity of<br>native ungulates                  | +0.685   | 0.010             | 46.9        |
| Elevation                                                 | -0.595   | -0.0009           | 11.0        |
| Sand %                                                    | +0.285   | 0.015             | 11.1        |
| Grazing intensity<br>of horses                            | +0.155   | 0.034             | 9.8         |
| <i>Poa pratensis</i><br>Cover ( $Y_3$ )                   |          | Constant = 6.091  | TVA = 57.0% |
| Soil moisture at<br>23 cm                                 | +0.467   | 0.086             | 21.8        |
| Permanent wilting<br>percentage 23 cm                     | -0.023   | -0.066            | 8.9         |
| Grazing intensity<br>of native ungul-<br>ates             | -0.447   | -0.0091*          | 11.7        |
| Elevation                                                 | +0.007   | -0.00091          | 6.0         |
| Free lime at<br>8 cm                                      | -0.346   | -0.321            | 8.6         |
| <i>Antennaria nitida/</i><br><i>rosea</i> Cover ( $Y_4$ ) |          | Constant = 2.021  | TVA = 77.3% |
| Free lime at<br>8 cm                                      | +0.592   | 0.853             | 35.0        |
| Silt %                                                    | -0.412   | -0.051            | 18.6        |
| Available water<br>at 23 cm, %.                           | -0.111   | 0.060             | 5.2         |



TABLE 28. Cont'd.

|                                               |                   |          |             |
|-----------------------------------------------|-------------------|----------|-------------|
| Av. Potassium at<br>8 cm                      | -0.174            | 0.0032   | 4.2         |
| Av. nitrogen at<br>8 cm                       | -0.218            | -0.099   | 3.3         |
| Grazing intensity<br>of native ungul-<br>ates | -0.003            | 0.064    | 5.6         |
| Slope aspect                                  | +0.390            | -0.882   | 5.4         |
| <i>Astragalus striatus</i><br>Cover ( $Y_4$ ) | Constant = -0.254 |          | TVA = 49.0% |
| Free lime at 8 cm                             | +0.507            | 0.276    | 25.6        |
| $\sqrt{\text{Gravel}}$ %                      | +0.214            | 0.164    | 13.6        |
| Soil moisture<br>at 23 cm, %.<br><2 mm basis  | -0.364            | -0.015   | 9.8         |
| <i>Artemisia frigida</i><br>Cover ( $Y_6$ )   | Constant = 2.959  |          | TVA = 76.7% |
| Grazing intensity of<br>native ungulates      | +0.676            | 0.0059   | 45.7        |
| Elevation                                     | -0.518            | -0.00049 | 6.1         |
| Clay %                                        | -0.212            | -0.035   | 4.0         |
| $\sqrt{\text{Gravel}}$                        | -0.367            | -0.105   | 7.6         |
| Time of sampling                              | +0.188            | 0.021    | 4.3         |
| Total angiosperm<br>Cover - $Y_6$ , %         | -0.406            | -0.0085  | 4.5         |
| Soil moisture at<br>20 cm, <2 mm,<br>% basis  | -0.318            | 0.011    | 4.5         |
| <i>Total Angiosperm</i><br>Cover %            | Constant = -13.05 |          | TVA = 64.4% |
| Time of sampling                              | +0.567            | 0.866    | 32.1        |
| Av. phosphorus at<br>8 cm                     | +0.333            | 2.050    | 18.5        |
| Free lime at 60 cm                            | +0.102            | 9.120    | 6.7         |
| Field capacity at<br>23 cm                    | +0.361            | 0.729    | 7.1         |

For explanation of terms and symbols, see footnotes to Table 15, p.174.



*montanensis* Grasslands. The lowest "r" value between any two species in this group was between *Artemisia* and *Astragalus* (+0.21). All four species were negatively correlated with *Poa pratensis* but the correlations were not significant at the 5% level; the negative *Poa-Koeleria* and *Poa-Artemisia* correlations were significant at the 10% probability level. *Agropyron dasystachyum* was not significantly correlated with any of the other five selected species, as in the Hay Meadow intensive study site at Waterton (p. 197).

## 2. Inter-environmental Correlations

Eighty-five of the 253 environmental pairings were significantly correlated at the 5% probability level (Table 27). This shows that almost none of the 23 environmental factors measured acts independently. Instead, they form an environmental complex and many of the simple correlations are therefore impossible to explain without reference to the complex as a whole. Many of the correlations are to be expected, *e.g.*, clay content is correlated positively with Field Capacity, sand content negatively with Field Capacity, and field soil moisture (as % of <2 mm fraction, and as % of <2 mm fraction—PWP) positively with elevation. However, some correlations result from non-random stand sampling (*e.g.*, date of sampling correlates positively with N-facing slopes, S-facing slopes negatively with slope angle) and result in other apparently meaningless correlations, *e.g.*, slope angle positively with Field Capacity and





### Permanent Wilting Percentage.

"Date of sampling" was included in this correlation study so that allowance was made for phenological effects resulting from a time difference of two months between the sampling of the first and the last stands. Date of sampling was correlated positively with total angiosperm cover and negatively with all three field soil moisture variables (Nos. 12, 13 and 17). Total angiosperm cover increased significantly from June 20 to August 23 in 1967 and soil moisture at 23 cm decreased significantly over the same period. Total angiosperm cover was also correlated positively with Field Capacity, probably because of the proportion of clay-humus at that depth. Soils with a low clay-humus content tend to have lower standing crops and perhaps also productivity.

The pellet group count for native ungulates, mostly elk, was positively correlated with free lime content and pH at 8 cm and negatively correlated with elevation, available phosphorus and potassium and field soil moisture. These correlations agree with field observations that the heaviest grazing by elk was in grasslands at lower elevations; the soils of these sites are driest, have most free lime near the surface and have least available potassium and phosphorus. They are probably also the least productive.

Fecal count for horses was correlated positively with both available nitrogen and elevation.



The Red Deer River valley stands (Nos. 21, 30, 31) were the most heavily grazed by horses and were at higher elevations than many of the other stands.

Soils at higher elevations tended to have relatively high concentrations of available nutrients, especially nitrogen and phosphorus at 8 cm, and high soil moisture at 23 cm when correction was made for the high gravel content.

The three field soil moisture variables (Nos. 12, 13 and 16, Table 26) were strongly positively correlated with each other and also with Field Capacity and Permanent Wilting Percentage. The soils at lower elevations were mostly very xeric Orthic Regosols and had very thin A horizons, little profile development and sandy textures, hence low moisture-holding capacities. Soil moisture was also positively correlated with available nitrogen and phosphorus, indicating that soils at high elevations tend to be less deficient in these two nutrients.

Field Capacity, Permanent Wilting Percentage and available water content were all positively correlated with each other and with clay, silt and available phosphorus and potassium concentrations, and negatively correlated with pH at 8 cm, and sand and free lime contents. Soils with a high proportion of clay and silt in their mineral fractions have relatively high moisture-holding capacities and greater retention of nutrients than do sandy soils. The negative correlations of Field Capacity and Permanent Wilting Percentage with both pH and free lime content





probably result from the negative correlation of elevation with coarse-textured soils and soils with high lime contents. Calcareous soils with high pH values near the surface (*i.e.*, those in the arid *Koeleria-Calamagrostis montanensis* Grasslands) tend to have low available phosphorus and potassium concentrations.

### 3. Vegetation and Environment

Simple correlation showed that total angiosperm cover increased significantly with date of sampling during the summer of 1967 and with the Field Capacity of the soil at 23 cm. However, multiple regression equations indicated that the levels of available phosphorus and free lime are also important in determining the total angiosperm cover (Table 28), relationships which are not evident at the simple correlation level. The following terms together accounted for 64% of the variation in total angiosperm cover: time of sampling, free lime at 60 cm, available phosphorus at 8 cm and Field Capacity at 23 cm. It is notable that neither the intensity of grazing by native ungulates nor by horses (as indicated by fecal counts) were significantly correlated with total angiosperm cover.

There were no significant correlations between *Agropyron dasystachyum* cover and any of the environmental factors measured, and the three significant terms in the multiple regression equation of *Agropyron* cover accounted for only 31% of the variation in this species. The three



significant terms — slope angle, free lime at 60 cm and available water at 23 cm — indicate that *Agropyron* in Banff and Jasper National Park grasslands is most abundant on slopes and on soils with high available water capacity, and with B and C horizons with high free lime contents.

The cover of *Poa pratensis* was correlated positively with soil moisture and negatively with grazing intensity by ungulates—*i.e.*, this species occurs mainly on mesic sites with little or no grazing by elk in the study areas. The multiple regression equation of *Poa pratensis* cover had five significant terms which, however, accounted for only 57% of the variation. The three terms which do not appear in simple correlations are Permanent Wilting Percentage at 23 cm, free lime at 60 cm, and elevation. The addition of the two latter terms as terms 4 and 5 made the third term (grazing intensity of native ungulates) insignificant (Table 28). Thus, the cover of *Poa pratensis* in the study area is higher at low elevations and on soils with high moisture contents but low Permanent Wilting Percentages at 23 cm, and with low free lime contents at 8 cm.

The cover of *Koeleria cristata* was significantly correlated with 11 environmental variables, many of which were correlated strongly with each other in the form of an environmental complex. The multiple regression equation of *Koeleria* cover had four terms and accounted for 79% of the variation in its cover. Two of these four terms — sand % and the intensity of grazing by horses — were



not significantly correlated with the dependent variable at the simple level. Since the equation takes inter-environmental correlations into account, it shows that four factors alone can account for the variation in the cover of *Koeleria cristata*. *Koeleria* occurs most abundantly in areas that are grazed by native ungulates and horses, where it acts as an "increaser", and on sandy soils at low elevations. Such soils tend to have low soil moisture contents, Field Capacities and available phosphorus; high pH values and free lime contents; and low total angiosperm covers; thus accounting for the multiplicity of simple correlations with *Koeleria* cover.

*Antennaria nitida/rosea*<sup>24</sup> was significantly correlated with 13 of the environmental variables and had the same type of relationship with 9 of them as did *Koeleria cristata*. Thus, *Antennaria* seems to be very similar to *Koeleria* in many of its environmental requirements, as would be expected from their high degree of positive association. However, only four of the terms in the 7-term multiple regression equation of *Antennaria* had significance as simple correlations (slope aspect, free lime and available phosphorus at 8 cm, and silt %), the relationships with the other three terms (available water, available nitrogen and intensity of grazing by horses) having been obscured by inter-environmental correlations at the simple level.

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<sup>24</sup> See footnote, p. 59





The equation accounted for 77% of the variation in *Antennaria* cover; the seven terms accounted for much of the distribution and abundance of this species. It seems to act as an "increaser" in sites grazed by horses but not in those grazed by elk. There is a complex of inter-related factors determining the distribution of *Antennaria* and no one factor is of paramount importance.

The cover of *Astragalus striatus* was significantly correlated with eight environmental variables, only two of which (free lime at 8 cm and soil moisture %) were represented in the 3-term multiple regression equation of this species. This equation accounted for only 49% of the variation. The third significant term in the equation was " $\sqrt{\text{Gravel\%}}$ ". *Astragalus striatus* occurs on soils with free lime in the A horizon, low moisture and high gravel content.

The cover of *Artemisia frigida* was significantly correlated with seven environmental variables, four of which were in the 7-term multiple regression equation. This equation accounted for 77% of the variation in the cover of this species. *Artemisia* acts as an "increaser" under heavy grazing by native ungulates, mostly elk. It is most abundant at low elevations in sites with low angiosperm cover and on soils with low clay and gravel contents. *Artemisia* is the last species to flower in the *Koeleria-Calamagrostis montanensis* Grasslands and is the only one of the six species selected which has date



of sampling as a significant term in the regression equations. When corrected for date of sampling, the negative correlation of *Artemisia* with soil moisture at the simple level becomes a positive correlation in the multiple regression equation. It seems, therefore, that *Artemisia* is increased by higher soil moisture, and occurs most abundantly in heavily-grazed grasslands.

Although *Koeleria cristata*, *Antennaria nitida/rosea*<sup>2 5</sup>, *Astragalus striatus* and *Artemisia frigida* are four of the Dominant species in *Koeleria-Calamagrostis montanensis* Grasslands and have in common many simple correlations with the environment, multiple regression has shown that the environmental variables are differentially important to the four species.

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<sup>2 5</sup> See footnote, p. 59





## INTEGRATION

Comparisons between the grasslands studied in Banff, Jasper and Waterton Parks will now be made with regard to the following: vegetational discontinuity, climate and topography, grassland type, structure and species composition, standing crop and effects of grazing, and soil characteristics.

It has been shown by means of three-dimensional ordination and cluster analysis that a clear floristic separation exists between the grasslands at low elevations in Banff and Jasper and those in Waterton. Ogilvie (1962) also found in Alberta a major floristic discontinuity between the most southerly part of the Rocky Mountains and the rest of these mountains.

The Waterton grasslands are more moist and temperate for most of the year than those in Banff and Jasper. Waterton lies in a "storm-track" belt in which maritime influences from the W coast are brought far inland (Daubenmire, 1943; Ogilvie, 1962). Thus, Waterton has a higher total precipitation and milder temperatures than Banff and Jasper. Most of the Banff and Jasper stands are in mountain valleys, where there is a rain shadow effect, and receive only 15-18 inches of precipitation annually, *c.f.* the Waterton stands which are mostly in foothills and receive 26 inches or more. Waterton has only one month of moisture deficits in summer whereas



Banff and Jasper have 2-3 months.

The milder, wetter climate in Waterton results in higher standing crop and probably higher productivity, and accounts at least in part for the large number of species Differential to the grasslands in this Park.

When elevation is compensated for latitude, the small "Park"-like grasslands (*sensu* Daubenmire, 1943) sampled in the Bow and Red Deer River valleys in Banff are at much higher elevations than the more extensive grasslands of the Athabasca River valley in Jasper. The latter grasslands have a more continental climate with warmer summers and slightly colder winters than the grasslands in Banff. They also have lower total precipitation. Moisture deficits appear in the Athabasca valley soils in the growing season about a month earlier than in those in Banff and 2 months earlier than in those in Waterton.

Thus, the grassland habitats of the Athabasca valley have the longest period of summer drought and are the most xeric in this study.

The following grassland types have been recognized and described: *Festuca-Danthonia* Prairie, Grass Meadows and Sedge Meadows (Waterton); *Koeleria-Calamagrostis montanensis* Grasslands, and *Stipa richardsonii* Subalpine Grassland (Banff and Jasper); *Koeleria-Geum triflorum* Grassland and *Elymus innovatus* Subalpine Shrub Savanna (Banff); and *Poa-Hordeum jubatum* Grassland (Jasper).





All the Waterton grasslands and the more mesophytic of those in Banff and Jasper are identified as seasonal, orthophyll, short-grass meadows, while the remaining stands are either seasonal grass steppe (at low elevations) or deciduous, orthophyll shrub savanna (at higher elevations) (Fosberg, 1967).

When latitudinal differences are compensated for by correcting all stands to the latitude of the most southerly (No. 15, 49° 2'N), the grassland types can be arranged in a sequence from low to high elevation as follows: Waterton Grass and Sedge Meadows (4,200-4,300 ft); *Festuca-Danthonia* Prairie (4,200-5,000 ft); *Koeleria-Calamagrostis montanensis* Grassland (4,900-5,300 ft) and *Poa-Hordeum jubatum* Grassland (5,000-5,100 ft); *Koeleria-Geum triflorum* Grassland (5,400-6,800 ft), *Stipa richardsonii* Subalpine Grassland (5,600-6,300 ft), and *Elymus innovatus* Subalpine Shrub Savanna (6,200-6,400 ft).

However, the significance of this elevational sequence is limited due to the following environmental factors which modify Daubenmire's (1943) zonation of the Rocky Mountains based on large scale temperature and precipitation effects. (a) There are great differences in macroclimate between Waterton and the other two Parks. (b) Most of the grasslands are on or close to the basal plains of the main river valleys and are therefore subject to special climatic effects associated with topographic position rather than elevation, *e.g.*, greater





diurnal range of temperature, strong valley winds and cold air drainage.

Thus, for example, although the *Koeleria-Calamagrostis montanensis* and the *Poa-Hordeum jubatum* Grasslands are at higher elevations than the *Festuca-Danthonia* Prairie, the last are considerably more mesophytic, instead of more xerophytic as would be expected from Daubenmire's (1943) principles.

Therefore, in this study, variations in environment, and consequently in grassland type, due to elevational differences alone, can be considered only within relatively small areas, *i.e.*, within each Park, and latitudinal differences can then be largely disregarded. On this basis, the *Koeleria-Calamagrostis montanensis* and *Poa-Hordeum jubatum* Grasslands are the lowest in elevation in Banff and Jasper Parks. The former are on medium-to coarse-textured soils and are the most xerophytic type in the two Parks. The *Koeleria-Geum triflorum* Grasslands, *Stipa richardsonii* Subalpine Grasslands, and the *Elymus innovatus* Shrub Savanna are at much higher elevations in these Parks. The vegetational differences between these three grassland types may be attributed to such non-elevational effects as local topography, grazing history, soil parent material, and local climatic variations.

The following three well-defined strata compose the *Festuca-Danthonia* Prairie: tall forb-bunch grass, low forb-grass understory, and a mat-like ground cover



of mosses, *Selaginella* and small forbs. The tall forb-bunch grass stratum is Dominant in the more mesic areas such as depressions and N-facing slopes, while the two lower strata are Dominant in more xeric areas such as ridge tops, S-facing slopes and very gravelly areas. Thus, the vegetation structure is primarily controlled by the moisture and heat régimes of the soil layers in contact with the vegetation. These findings are in agreement with the observations of Ayyad and Dix (1964). Grazing also tends to eliminate the tall forb-bunch grass stratum.

In the *Koeleria-Calamagrostis montanensis* Grasslands, few species are taller than 20-25 cm and there is no stratum corresponding to the tallest in the *Festuca-Danthonia* Prairie. The vegetation structure resembles that in the most xeric and heavily-grazed prairie sites, with sparse representation of the two lower strata only.

Usually, the *Koeleria-Geum triflorum* Grasslands have only the two lower strata although there are scattered species in the tall forb-bunch grass stratum in the most mesic sites.

No clear structure is evident in the *Poa-Hordeum jubatum* Grasslands.

Both the *Stipa richardsonii* Subalpine Grasslands and *Elymus innovatus* Subalpine Shrub Savanna have a well-developed but open shrub stratum, an ill-defined lower stratum of medium-sized grasses and forbs, and often a mat-like ground cover composed predominantly of





*Arctostaphylos uva-ursi*.

*Festuca scabrella*, the Dominant species in the more mesic *Festuca-Danthonia* Prairie sites, is sparse in many of the Banff stands and absent in the Jasper stands. Many of the Banff stands are grazed by elk and horses, and it is possible that *Festuca scabrella*-Dominated grassland would develop in some of these areas if grazing were eliminated.

*Danthonia parryi*, *Festuca idahoensis* and *Selaginella densa*, which are co-Dominants in the *Festuca-Danthonia* Prairie, act as "increasers" (*sensu* Johnston *et al.*, 1966) and are Dominants in the more xeric sites.

Thus, *Festuca-Danthonia* Prairie seems to be a mosaic of edaphic climaxes composed of *Festuca scabrella* and *Danthonia intermedia* in the most mesic sites, *F. idahoensis* and *Danthonia parryi* in the intermediate sites, and *F. idahoensis*, *Koeleria cristata* and *Selaginella densa* in the xeric, exposed sites.

*Danthonia intermedia* is a Dominant in both *Festuca-Danthonia* Prairie and *Stipa richardsonii* Subalpine Grassland, but is usually absent in the other grassland types. It seems to require high soil moisture, and in the *Festuca-Danthonia* Prairie grasslands occurs on N-facing slopes and in depressions, where *Festuca scabrella* is most abundant, *i.e.*, in sites with moisture régimes closest to that in the *Stipa richardsonii* Grassland "Parks" (*sensu* Daubenmire, 1943). The latter Grasslands are grazed very



little and there is no apparent reason for the sparse cover and lack of Dominance of *Festuca scabrella* in this grassland type.

Most of the Dominants in the *Koeleria-Calamagrostis montanensis* Grasslands are widespread and act as "increasers" in areas grazed by elk and horses in stands of the other grassland types, e.g., *Artemisia frigida* (c.f. Bird, 1961), *Antennaria nitida*, *Erigeron caespitosus* and *Koeleria cristata*. Although *Koeleria* has a shallow root system, it seems to tolerate low soil moisture contents and is especially prominent on sandy soils at low elevations. *Koeleria* and *Agropyron dasystachyum* appear to be opportunist species in the Hay Meadow area in Waterton in sites too dry for the usual Dominants. In Waterton, *Agropyron dasystachyum* occurs mainly on low-lying alluvial soils with alkaline Ah horizons. In Jasper, on the highly calcareous soils of the Athabasca River valley, it increases under protection and is perhaps one of the major "decreasers" (*sensu* Johnston *et al.*, 1966) in the *Koeleria-Calamagrostis montanensis* Grasslands.

*Koeleria-Geum triflorum* Grasslands have many species in common with both *Koeleria-Calamagrostis* Grasslands and *Festuca-Danthonia* Prairie and are geographically intermediate between these two types.

Some of the Dominants in the *Stipa richardsonii* Subalpine Grasslands and all of those in the *Elymus innovatus* Subalpine Shrub Savanna are understory species



common in coniferous forests.

Also, many species prominent in the *Stipa* grasslands are common but not Dominant in the most mesic *Festuca-Danthonia* Prairie sites, e.g., *Agropyron trachycaulum* var. *unilaterale*; *Danthonia intermedia*, *Poa pratensis*, *Stipa richardsonii* and *Penstemon confertus*. It is notable that the soils of the *Stipa richardsonii* Grasslands did not develop as large late-summer moisture deficits as soils of the other grassland types.

*Poa pratensis* is abundant on moist, cool, non-gravelly soils. Its widespread occurrence and lack of specificity to any grassland type suggest an opportunist species. It has probably been spread by horses to most areas. Under moderate grazing pressure, it acts as an "increaser" and often forms pure stands (Bird, 1961). *Poa pratensis* acts as an increaser in forest stands in E Washington and N Idaho. It seems to be a good indicator of the maximum intensity of past grazing, since, on cessation of grazing, native species do not regain control although further increase of *Poa* is halted (Daubenmire and Daubenmire, 1968).

In the standing crop studies, the highest values were found in the *Stipa richardsonii* Grassland site at Hillsdale. Slightly lower values were found for the *Festuca-Danthonia* Prairie sites in Waterton. The lowest value was found in the *Koeleria-Calamagrostis* Grassland site (Henry House). The *Stipa richardsonii* Grassland site





had by far the greatest standing crop of "graminoids" whereas the three *Festuca-Danthonia* Prairie sites had the greatest standing crops of forbs.

The following sites have all been heavily grazed by elk and/or horses for many years and had the four lowest standing crop values recorded: Henry House (*Koeleria-Calamagrostis* Grassland); Tyrrell Creek (*Koeleria-Geum* Grassland); Banff airstrip (intermediate between *Koeleria-Calamagrostis* and *Koeleria-Geum*); and Stoney Creek (*Festuca-Danthonia* Prairie). Comparisons between these sites indicate that the *Festuca-Danthonia* Prairie at Waterton is far more productive than the *Koeleria-Calamagrostis* Grasslands and slightly more productive than the *Koeleria-Geum* Grasslands. However, little reliance should be placed on the very limited results of this study.

Comparisons of potential productivity and the differential effects of long-term grazing can be made by reference to the seven enclosure plots.

The highest standing crop values inside the enclosures were at the *Festuca-Danthonia* Prairie sites (Badlands, Lookout Butte), and the lowest in two of the *Koeleria-Calamagrostis* Grassland sites (Moberly, Henry House). The highest standing crop of "graminoids" was in the *Koeleria-Calamagrostis* Grassland site at Devona and the lowest in the *Koeleria-Calamagrostis* Grassland at Henry House. The Devona and Henry House results show that some but not all of the sites now occupied by uniformly sparse and xerophytic *Koeleria-Calamagrostis* Grassland



may, under grazing protection, develop into much more productive grassland.

In the three *Koeleria-Calamagrostis* Grassland sites, grazing protection results in an increase in the abundance of grasses, especially *Agropyron dasystachyum* and *Calamagrostis montanensis*. Leaf litter is also increased but build-up of the Ah horizon is slow. Xerophytic forbs, principally *Artemisia frigida*, decrease while the Dominant grass species, *Koeleria cristata*, is relatively unaffected. *Antennaria nitida* and *Astragalus striatus* increase under grazing protection in the more mesic sites.

The Hillsdale exclosure is not truly representative of *Stipa richardsonii* Grassland as there are no shrubs present and *Poa pratensis* forms the major part of the heavy grass cover at this site. This probably indicates heavy grazing in the past (Daubenmire and Daubenmire, 1968). However, results from this exclosure showed that complete protection from ungulate grazing can decrease productivity in very productive grasslands by causing excessive build-up of leaf litter.

Results from exclosure plots in Waterton showed that even light grazing of *Festuca-Danthonia* Prairie leads to replacement of the major Dominant, *Festuca scabrella*, by "increasers". This confirms the observations of Johnston (1961). The principal "increasers" were *Koeleria cristata* and *Tortula ruralis* at the lightly-grazed Badlands site, and *Koeleria*, *Erigeron caespitosus* and terricolous lichens such as *Cornicularia aculeata* and *Cladonia* sp. at the





heavily-grazed Stoney Creek site. At the latter site, other Dominant species, notably *Festuca idahoensis*, *Galium boreale* and *Monarda fistulosa* var. *menthaefolia* have decreased under elk grazing, and *Festuca scabrella* has been almost eliminated.

The soils of most of the *Festuca-Danthonia* Prairie and Waterton Grass and Sedge meadow stands are gravelly Orthic Black Chernozems characteristic of the Black Soil Zone in Alberta. The soils have ill-defined B horizons and tend to have much thinner Ah horizons on exposed, xeric sites (Rego Black Chernozems). Some appeared to be Dark Brown Chernozems, as might be expected from the proximity of the Dark Brown Soil Zone (Odynsky, 1962). The *Festuca-Danthonia* Chernozems have much higher concentrations of nitrogen, phosphorus and potassium than most of the soils in this study. The Ah horizon was neutral to alkaline in alluvial soils and acid in soils of glacial till origin.

Most of the soils of the *Koeleria-Calamagrostis* Grasslands are Orthic Regosols with thin, unstable Ah horizons, very calcareous profiles almost to the surface, and the lowest concentrations of available nutrients in any of the grassland soils in this study. The development of the *Koeleria-Calamagrostis* soils as Regosols results partly from many years of grazing of the xerophytic, short-grass vegetation, and partly from the dry climate.

It is doubtful if much of the Athabasca River valley now supporting *Koeleria-Calamagrostis* Grassland could



support a more mesic grassland such as the *Festuca-Danthonia* Prairie at Waterton *c.f.* results from Devona exclosure. Strong valley winds, especially in winter, and a dry climate together make the soil surface very unstable; most of the soils of the *Koeleria-Calamagrostis* Grasslands have either wind-eroded or -deposited surfaces.

The narrow valleys in which the *Poa-Hordeum jubatum* Meadows are situated probably have occasional spring flooding. This may in part account for the characteristically high clay content almost to the surface of the soils. *Poa-Hordeum jubatum* Meadows have poorly-developed (Regosolic) profiles.

Very few generalizations can be made regarding the soils of the other three grassland types because of the small numbers of stands and the limited extent of each type. Their soils are all products of specific, local environmental factors at relatively high elevations in mountain valleys and have little in common with each other even within the same grassland type.



## DISCUSSION AND CONCLUSIONS

In the Integration, the inter-relationships of the grassland types found in Banff, Jasper, and Waterton Lakes National Parks have been considered. The relationships of these grasslands to others described in the literature will now be discussed, and their status as vegetation types assessed.

The low-elevation grasslands in all three Parks occur east of the Continental Divide in the Rocky Mountains. They are in the main valleys of Banff and Jasper, and in the main valley foothills of Waterton.

The macroclimate of the three study areas is essentially continental in character, with long, cold winters, short summers, and maximum precipitation in early summer. Thus, the macroclimate of these low-elevation grasslands more closely resembles that of the grasslands of Alberta and Saskatchewan than that of the Palouse Prairie of interior British Columbia where, because of maritime influences, the climate is more moderate in temperature, and precipitation fairly uniformly distributed throughout the year (Can. Dept. Transport, 1962; Tisdale, 1947).

However, the local climates of the grasslands studied are governed by a number of other factors such as elevation, topographic position, strong valley winds and chinook warming, which cause great variability in climate within relatively short distances. Thus, the grasslands at low





elevations, especially those in Banff and Jasper, probably depend largely on local modifications of the macroclimate.

The Waterton area receives far more precipitation than any of the other major grassland areas in W Canada except Manitoba, but is subject to the drying effects of year-round strong valley winds which cause increased evapotranspiration, and winter chinooks. Therefore, the moisture availability may be equivalent to that in the more mesophytic types of grassland in W Canada, *e.g.*, the Fescue Prairie in Alberta (16-18 inches; Coupland, 1961) and the *Agropyron-Festuca* zone in S British Columbia (approximately 12-16 inches; Tisdale, 1947).

Most of the species prominent in the *Festuca-Danthonia* Prairie in Waterton are also prominent in the *Festuca-Danthonia* association of SW Alberta as described by Moss (1944). The Waterton prairie might therefore be considered part of this association. However, Coupland (1961) supported the modified view of Moss and Campbell (1947) that the *Festuca-Danthonia* association in SW Alberta is not the "virgin or climax grassland of the region" but results from mowing and grazing by cattle and horses. Further, *Festuca scabrella* usually outranks all other species sufficiently to warrant the inclusion of the pristine *Danthonia parryi*-dominated areas as an edaphic climax within the Fescue Prairie association of the N American prairies.

Also, the standing crop of ungrazed or lightly grazed *Festuca-Danthonia* Prairie in Waterton was of similar



magnitude to that reported by Johnston (1961) for the fescue prairie in Alberta.

However, as the following comparisons show, the *Festuca-Danthonia* Prairie in Waterton resembles other grassland types in British Columbia and NW USA almost as much as it does the Fescue Prairie association in W Canada.

The Fescue Prairie association has been described in Alberta (Moss and Campbell, 1947), in Saskatchewan (Coupland and Brayshaw, 1953), in Riding Mtn. National Park, Manitoba (Blood, 1966) and in North Dakota (Cosby, 1965). None of these descriptions bears a very close resemblance to the *Festuca-Danthonia* Prairie in Waterton, due to (a) the absence from them of such prominent Cordilleran species as *Agropyron spicatum*, *Danthonia parryi*, *Festuca idahoensis*, *Stipa columbiana*, *Geranium viscosissimum* and *Lupinus sericeus*, and (b) the lack of complete Dominance by *Festuca scabrella* in much of the Waterton prairies.

The *Festuca-Danthonia* Prairie seems to have close vegetational affinity with the Foothills Prairie (*Agropyron-Festuca-Stipa*) of Montana as described by K  chler (1964). *Festuca idahoensis*, *F. scabrella* and *Agropyron spicatum* are Dominants in the Foothills Prairie. The two *Festuca* species are Dominant and *Agropyron* prominent in the *Festuca-Danthonia* Prairie.

The *Festuca-Danthonia* Prairie also resembles fairly closely the *Festuca idahoensis* grasslands in S Montana (Wright and Wright, 1948) and in the Madison Range, Montana





(Patten, 1963) and the *Festuca idahoensis*-*Lupinus sericeus* association of the Bighorn Mountains, Wyoming (Hurd, 1961). Thirty nine of the 66 species listed by Hurd, including all five Dominants (*Festuca idahoensis*, *Koeleria cristata*, *Carex obtusata*, *Agoseris glauca* and *Lupinus sericeus*), are common and often prominent in the Waterton prairie.

Also, the standing crop of *Festuca*-*Danthonia* Prairie in Waterton is of similar magnitude to that reported by Hurd (1961) for the *Festuca idahoensis*-*Lupinus sericeus* association.

The *Festuca*-*Danthonia* Prairie is also closely related to the *Festuca*-*Agropyron* zone in the Palouse Prairie of Washington and Idaho (Daubenmire, 1942) and to the *Agropyron*-*Festuca* zone in S-central British Columbia (Tisdale, 1947) which is vegetationally very similar to the *Festuca*-*Agropyron* zone. These last two vegetation types are on Black Chernozemic soils. The following species are prominent in all three grassland types: *Agropyron spicatum*, *Festuca idahoensis*, *F. scabrella* (absent from the *Festuca*-*Agropyron* zone), *Koeleria cristata*, *Stipa columbiana*, *Balsamorhiza sagittata*, *Galium boreale*, *Geranium viscosissimum*, *Lithospermum ruderale*, *Lupinus sericeus* and *Solidago missouriensis*. Six of these species are considered of Palouse Prairie origin by Moss (1944)

Thus, the species composition of the *Festuca*-*Danthonia* Prairie in Waterton seems to be a mixture of species prominent in the *Festuca scabrella* association of the Canadian



Prairies, the *Festuca idahoensis* grasslands and Foothills Prairie of Montana and Wyoming, and the Palouse Prairie of British Columbia, Washington and Idaho. The great species diversity in the Waterton prairie is due not only to the climatic influences but also to strong Cordilleran and Boreal influences. Ogilvie (1962) lists a large number of Cordilleran species restricted to the SW part of Alberta.

The *Festuca-Danthonia* Prairie in Waterton is a mosaic of edaphic climaxes and only in the most mesic and ungrazed sites is *Festuca scabrella* predominant. Over most of the area, *Danthonia parryi* and *Festuca idahoensis*, because of their greater tolerance of xeric, exposed sites are Dominant, or co-Dominant with *Festuca scabrella*. *F. scabrella* is very sensitive to grazing, a factor which can be regarded as "natural" and constantly affecting these grasslands.

It therefore seems reasonable to regard the *Festuca-Danthonia* Prairie at Waterton as a mosaic of edaphic-topographic climaxes which together form the *Festuca-Danthonia* association as described by Moss in 1944.

The Waterton Grass and Sedge meadows have, over a long period, been occasionally cut for hay, and "hay grasses" such as *Bromus inermis*, *Festuca elatior* and *Phleum pratense* may have been sown in parts of the meadows. Other species such as *Poa pratensis*, *Ranunculus acris*, *Trifolium pratense* and *T. repens* may have been accidentally introduced by man or horses. Although some of the Dominant species are native, e.g., *Carex praegracilis*, *Juncus balticus*, *Fragaria*





*virginiana* var. *glauca*, *Pedicularis groenlandica* and *Thalictrum venulosum*, a large proportion of these Meadows are not in a pristine state. It is probable that the Meadow vegetation would be succeeded by the adjacent willow or poplar vegetation if mowing were discontinued.

Thus, the Waterton Grass and Sedge meadows cannot be regarded as representative of any native vegetation type. They are communities resulting from disturbance by man. Furthermore, these Meadows were not sampled extensively as they did not fit the selection criteria strictly. Therefore, no comparisons will be made with other grassland types described in the literature.

Most of the *Koeleria-Calamagrostis montanensis* Grassland is in the Athabasca River valley in Jasper Park and is geographically isolated from any other grasslands described in the literature. This geographic isolation partly accounts for the low degree of resemblance between this grassland and the important grasslands spatially closest to it.

The *Koeleria-Calamagrostis* Grasslands have very little similarity to the *Festuca scabrella* association of the Canadian Prairies (Moss and Campbell, 1947; Coupland and Brayshaw, 1953; Coupland, 1961; Blood, 1966); to the Palouse Prairie in British Columbia and NW USA (Daubenmire, 1942; Tisdale, 1947); the Fescue-Snowberry association of E British Columbia (McLean and Holland, 1958); the Peace River grasslands (Moss, 1952); and the *Festuca idahoensis* grasslands and Foothills Prairie of Montana and Wyoming





(Wright and Wright, 1948; Hurd, 1961; Patten, 1963; Kuchler, 1964).

The *Koeleria-Calamagrostis* Grassland has a much greater similarity to the grazing disclimaxes or preclimaxes (*sensu* Clements, 1936) of these grassland types. It is notable that three of the five species Dominant in the *Koeleria-Calamagrostis* Grassland (*Koeleria cristata*, *Antennaria nitida*, *Artemisia frigida*) and many of the prominent species such as *Agropyron dasystachyum* and *Salsola kali* var. *tenuifolia* are very widely distributed species of xerophytic grasslands and grazed and disturbed sites throughout W Canada and NW USA. Coupland (1950) states that *Koeleria* is not highly drought-resistant but that it re-seeds bare areas readily and begins growth early in spring when the moisture supply is usually greatest. *Koeleria* was the most Constant species throughout all the grasslands in this study. *Artemisia frigida* is the most abundant forb of the Mixed Prairie association in W Canada and can tolerate considerable drought (Coupland, 1950). The other two Dominants of the *Koeleria-Calamagrostis* Grassland, *i.e.*, *Calamagrostis montanensis* and *Astragalus striatus* are apparently not Dominants in any other grassland type in W Canada.

The *Koeleria-Calamagrostis* Grassland type is linked to the heavily grazed areas of the Fescue-Snowberry association of E British Columbia by the prominence of *Calamagrostis montanensis*, *Koeleria cristata*, *Antennaria nitida* and *Artemisia frigida* (McLean and Holland, 1958); to the drier



of the Peace River grasslands by the prominence of *Agropyron dasystachyum*, *Koeleria cristata*, *Carex obtusata*, *Anemone patens* var. *wolfgangiana*, *Artemisia frigida* and *Solidago decumbens* (Moss, 1952), and to the stabilised sand dune and blowout communities in Saskatchewan by the prominence of *Agropyron dasystachyum*, *Calamagrostis montanensis*, *Festuca saximontana*, *Koeleria cristata*, *Carex eleocharis* and *Artemisia frigida* (Hulett et al., 1966).

The species prominent in the *Koeleria-Calamagrostis* Grasslands, the low values recorded for standing crop, and perhaps also the presence of *Stipa comata* in stand 47 and in the Devona exclosure area, indicate that these grasslands are less closely linked to the geographically-closer *Festuca scabrella* association than to some of the grasslands of the Mixed Prairie association (Coupland, 1950, 1961), notably the *Stipa-Agropyron* faciation on intermediate-textured soils in the Dark Brown Soil Zone and the *Agropyron-Koeleria* faciation on lacustrine clay soils in the Brown Soil Zone.

Also, the standing crop values for the *Koeleria-Calamagrostis montanensis* Grasslands were of similar magnitude to those recorded for mixed prairie by Coupland (1961) and Smoliak (1965) but were much lower than those recorded for fescue prairie by Johnston (1961) and Johnston et al. (1966). However, since the Mixed Prairie Dominants *Agropyron smithii*, *Bouteloua gracilis* and *Stipa spartea* var. *curtiseta* are absent in the *Koeleria-Calamagrostis* Grasslands, the resemblance is not a close one.





Coupland (1961) pointed out that grazing of the Fescue Prairie leads to an increase in the abundance of species of the *Stipa-Agropyron* faciation. Smoliak (1965) found that, in the Mixed Prairie in SW Alberta, light grazing increases many "short grass" species such as *Koeleria cristata* and *Agropyron dasystachyum* at the expense of the "mid grasses". The results of exclosure plot studies show that some parts of the *Koeleria-Calamagrostis* Grasslands may, under grazing protection, develop into a more mesophytic grassland type with much higher standing crops, especially that of grasses. Certain species, e.g. *Agropyron dasystachyum*, hitherto not Dominant, may thus attain Dominance.

Therefore, the *Koeleria-Calamagrostis* Grassland could probably be considered as resulting from heavy grazing of some other as yet undetermined climax vegetation type. It is dominated by "increaser" species which are usually very drought-tolerant and widespread in W Canada.

In the Athabasca River valley in Jasper, the mean annual precipitation (16 inches) is intermediate between that of the *Stipa-Agropyron* faciation of the Mixed Prairie (14-16 inches) and that of the *Festuca-scabrella* association (16-18 inches) (Coupland, 1961). The vegetation composition of the *Koeleria-Calamagrostis* Grassland indicates a slightly closer relationship with the *Stipa-Agropyron* faciation. A great decrease in grazing intensity could result in a grassland where *Koeleria cristata* and the "increaser" forbs were



reduced to sub-Dominant status, and *Agropyron dasystachyum*, *Stipa comata*, and perhaps *Calamagrostis montanensis* became Dominant. This would be very similar to parts of the *Stipa-Agropyron* faciation (Coupland, 1950, 1961).

In Jasper, however, between the xerophytic *Koeleria-Calamagrostis* Grasslands and the adjacent montane coniferous forest, there is no intermediate, more mesophytic grassland type such as the *Festuca scabrella* association. The ecotonal areas are occupied by coniferous savanna. North of Jasper townsite, the plain of the Athabasca River valley is occupied by a mosaic of xerophytic grassland, savanna and coniferous forest, and even at higher elevations no equivalent of the *Festuca scabrella* association was found.

Thus, within the Athabasca River valley, the normal macroclimatic zonal sequence found in Alberta of xerophytic grassland→mesophytic grassland→?aspen parkland→coniferous forest does not seem to apply. The *Koeleria-Calamagrostis* Grassland, therefore, does not seem to be an outlier of the Mixed Prairie Association.

The *Koeleria-Calamagrostis* Grassland is apparently a secondary zootic climax (Daubenmire, 1952) of a more productive vegetation type and has probably increased in extent as a result of increased burning and disturbance by man in the late 19th and early 20th centuries. There is at present no encroachment of forest on to grassland, and in a few places the lack of tree regeneration and the poor condition of the pine trees seem to be favoring the extension of this





steppe-like grassland. Protection from fire since the establishment of Jasper as a National Park has not resulted in any apparent extension of the forest, perhaps because of the combined effects of a microclimate of marginal suitability and trampling, browsing and grazing by ungulates. Also, the climate may have become more favorable to the development of grasslands than forests in the past half century because of a slight increase in temperature, evidence of which is, for example, the retreat of glaciers.

Thus, the *Koeleria-Calamagrostis* Grasslands seem to result from a complex of such environmental factors as dry climate, fire and other disturbances, and heavy grazing acting on very well drained soils.

The *Koeleria-Geum triflorum* Grasslands in Banff National Park seem to be most closely related to the *Koeleria-Calamagrostis* Grasslands, mainly because of the prominence of "increaser" species such as *Koeleria cristata*, *Carex eleocharis* and *Antennaria nitida*. Due to the prominence of *Helictotrichon hookeri*, *Cerastium arvense*, *Geum triflorum* and *Selaginella densa*, and the presence of *Festuca scabrella*, they also have some affinities with the *Festuca-Danthonia* Prairie in Waterton.

There is very little resemblance between the *Koeleria-Geum* Grasslands and the other grassland types at approximately the same elevation in Banff, i.e., the *Stipa richardsonii* Subalpine Grasslands and the *Elymus innovatus* Subalpine Shrub Savanna. No precipitation records are available for





the Red Deer River valley but it is probably in a rain shadow. This would result in a drier climate, elevation of the vegetation zones and development of a vegetation type much more xerophytic than those in valleys at similar elevations further W in the Rocky Mountains where the *Stipa richardsonii* and *Elymus innovatus* grasslands are located. It is notable that stand 33 outside the Red Deer River valley, although at a much lower elevation, was on a heavily-grazed, xeric site.

The *Koeleria-Geum* Grasslands have little in common with any of the published accounts of other grasslands in W Canada and NW USA. They are linked to the *Koeleria-Calamagrostis* Grasslands by the prominence of widely-distributed "increaser" species. They are also related to the more xeric and heavily-grazed areas in the *Festuca scabrella* association by the prominence of *Koeleria cristata*, *Carex eleocharis*, *Antennaria nitida* and *Selaginella densa*.

Although the high proportion of "increaser" species and the low standing crop values indicate a close relationship with the *Koeleria-Calamagrostis* Grasslands, the identity of the few "decreaser" species present indicates that the relationship with the *Festuca scabrella* association is the closer. Thus, the *Koeleria-Geum* Grassland seems to resemble most closely a zootic climax within the *Festuca scabrella* association, caused by heavy grazing by elk and horses.

The *Stipa richardsonii* Subalpine Grasslands are small "Parks" (*sensu* Daubenmire, 1943) surrounded by coniferous



montane or subalpine forest in the bottoms of mountain valleys in Banff and Jasper Parks. They have little similarity to any of the other grassland types in this study. Although some of the species prominent in this grassland are also prominent coniferous forest understory species, most are not, and the three most prominent shrubs (*Betula glandulosa*, *Potentilla fruticosa* and *Salix glauca*) are Differential.

There was usually no coniferous forest reproduction in the *Stipa richardsonii* Grassland stands. However, several areas at the same elevation, open because of disturbances such as fire, roadside clearances etc., had abundant spruce-fir-pine reproduction. No explanation for the presence of these small, apparently stable, *Stipa* grasslands within a coniferous forest zone was found in the present study. It seems probable that a complex of environmental and historical factors is involved.

Although the *Stipa richardsonii* Grasslands resemble the moister depressional areas of the *Festuca-Danthonia* Prairie in Waterton, and have a total standing crop value of similar magnitude, they do not seem to be closely related to the *Festuca scabrella* association as a whole. Most of the Dominants of this association do not occur in the *Stipa richardsonii* Grasslands, and *Festuca scabrella* was found only once (Hillsdale standing crop site).

The *Stipa richardsonii* Grasslands do not appear to have much in common with any of the other grassland types





described in W Canada or NW USA, except for the *Agropyron-Stipa* communities of the Peace River area (Moss, 1952), where *Agropyron dasystachyum*, *Danthonia intermedia* and *Stipa richardsonii* are also prominent.

It is concluded that the *Stipa richardsonii* Subalpine Grassland is related to the moister areas in the *Festuca scabrella* association and to the montane-subalpine coniferous forest understory but has, however, characteristics of its own, notably a well-developed and Differential shrub stratum. It seems to be a distinct grassland type characteristic of the moister sites in the Fescue Prairie-coniferous forest ecotone in Banff and Jasper Parks. However, the general absence of *Festuca scabrella* in these lightly-grazed or ungrazed areas is inexplicable on the basis of the present data. More extensive studies are needed to establish the climax status of the *Stipa richardsonii* Subalpine Grassland type.

The two stands of *Elymus innovatus* Subalpine Shrub Savanna sampled are examples of a vegetation type that is maintained primarily on steep, S-facing slopes in the mountains by frequent snow slides and occasional rock falls. Such disturbances prevent afforestation and cause the local environment to be much more xeric than is normal at that elevation.

Most of the species prominent in the *Elymus innovatus* Savanna are very common in the understory of montane and subalpine coniferous forest. The vegetation is therefore



composed of the more exposure-tolerant species of the nearby forest understory and a variable number of opportunist species.

The *Elymus innovatus* Subalpine Shrub Savanna is not, therefore, considered a distinct vegetation type.

The *Poa-Hordeum jubatum* Grasslands are not similar to any of the other grasslands in this study or to any other grasslands described in W Canada or NW USA. Their vegetation seems to consist of species which can grow on heavy, clay soils with possibly very variable moisture supply.

On the basis of the limited data from the present study, the *Poa-Hordeum jubatum* Grasslands cannot be considered a distinct grassland type. However, more extensive studies might establish them as of a grassland type characteristic of low-lying areas with clay soils, which lack trees because of periodic flooding.



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APPENDIX 1. LOCATIONS OF STANDS, SAMPLING DATES, AND  
TOPOGRAPHY.

| Stand           | Date<br>sampled | Latitude<br>o | (N)<br>' | Longitude<br>o | (W)<br>' | Mean<br>elevation<br>in ft. | Mean<br>aspect | Mean<br>slope<br>o |
|-----------------|-----------------|---------------|----------|----------------|----------|-----------------------------|----------------|--------------------|
| 1 <sup>1</sup>  | June 13         | 49            | 6½       | 113            | 53       | 4550                        | N 65 E         | 1                  |
| 2               | 15              | 49            | 5½       | 113            | 50½      | 4190                        |                | 0                  |
| 3               | 16              | 49            | 7        | 114            | 1        | 4790                        |                | 0                  |
| 4               | 17              | 49            | 6        | 113            | 58       | 4770                        | S 2 E          | 30                 |
| 5               | 18              | 49            | 4        | 113            | 50       | 4275                        |                | 0                  |
| 6               | 29              | 49            | 5        | 113            | 52½      | 4465                        |                | 0                  |
| 7               | July 1          | 49            | 7½       | 113            | 52½      | 4430                        |                | 0                  |
| 8               | 2               | 49            | 6½       | 113            | 53½      | 4670                        | N 85 E         | 8                  |
| 9               | 3               | 49            | 5        | 113            | 51       | 4270                        |                | 0                  |
| 10              | 3               | 49            | 5        | 113            | 51       | 4270                        |                | 0                  |
| 11              | 5               | 49            | 6        | 113            | 50½      | 4200                        |                | 0                  |
| 12              | 26              | 49            | 7½       | 113            | 49       | 4230                        |                | 0                  |
| 13              | 27              | 49            | 4        | 113            | 52       | 4210                        |                | 0                  |
| 14              | 28              | 49            | 10½      | 113            | 55½      | 4920                        | N 7 E          | 1                  |
| 15              | 29              | 49            | 2½       | 113            | 41½      | 4490                        |                | 0                  |
| 16              | 30              | 49            | 4        | 113            | 44       | 5130                        | S 58 W         | 5                  |
| 17              | 30              | 49            | 7        | 113            | 49       | 4230                        |                | 0                  |
| 18              | 31              | 49            | 6        | 113            | 57½      | 4570                        | S 34 E         | 3                  |
| 19              | Aug. 1          | 49            | 4½       | 113            | 49       | 4370                        | N 79 W         | 3                  |
| 20              | 2               | 49            | 9        | 113            | 52½      | 4940                        | S 52 E         | 5                  |
| 21 <sup>1</sup> | June 20         | 51            | 37       | 115            | 47       | 5565                        |                | 0                  |
| 22              | 21              | 51            | 14       | 115            | 49½      | 4715                        | S 18 W         | 1                  |
| 23              | July 7          | 51            | 16½      | 115            | 50       | 5410                        | S 60 E         | 1                  |
| 24              | 8               | 51            | 11       | 115            | 53½      | 5535                        | S 55 E         | 12                 |
| 25              | 9               | 50            | 54½      | 115            | 24       | 5350                        | S 72 W         | 5                  |
| 26              | 10              | 51            | 7        | 115            | 45       | 5385                        | S 38 E         | 26                 |
| 27              | 11              | 51            | 12½      | 115            | 32½      | 4560                        |                | 0                  |
| 28              | 12              | 51            | 10       | 115            | 26       | 4620                        |                | 0                  |
| 29              | Aug. 4          | 51            | 12       | 115            | 35½      | 5460                        | S 32 W         | 22                 |
| 30 <sup>2</sup> | 5               | 51            | 44       | 115            | 34       | 5040                        | West           | 4                  |
| 31              | 6               | 51            | 36½      | 115            | 49½      | 5720                        |                | 0                  |
| 32              | 8               | 51            | 10½      | 115            | 31½      | 4550                        |                | 0                  |
| 33              | 28              | 51            | 12       | 115            | 32½      | 4570                        |                | 0                  |
| 34              | 29              | 51            | 19       | 116            | 2½       | 4960                        |                | 0                  |
| 35              | 30              | 51            | 10½      | 115            | 33       | 4480                        |                | 0                  |
| 36 <sup>1</sup> | June 22         | 53            | 9        | 118            | 1        | 3245                        |                | 0                  |
| 37              | 23              | 53            | 8        | 118            | 1        | 3425                        | S 54 E         | 12                 |
| 38              | July 12         | 52            | 55½      | 118            | 1½       | 3365                        |                | 0                  |
| 39              | 15              | 53            | 9½       | 117            | 59½      | 3245                        |                | 0                  |
| 40              | 16              | 52            | 49½      | 118            | 2        | 3510                        |                | 0                  |
| 41              | 16              | 52            | 49½      | 118            | 2½       | 3505                        |                | 0                  |
| 42              | 17              | 53            | 3½       | 118            | 6½       | 3350                        | S 33 E         | 2                  |



## APPENDIX 1. Cont'd.

| Stand           | Date sampled | Latitude (N)<br>o | Longitude (W)<br>o | Mean elevation<br>in ft. | Mean aspect | Mean slope<br>o |          |
|-----------------|--------------|-------------------|--------------------|--------------------------|-------------|-----------------|----------|
| 43              | July 18      | 52                | 59½                | 118                      | 4           | 3305            | 0        |
| 44              | 19           | 53                | 13½                | 117                      | 56½         | 3305            | 0        |
| 45              | Aug. 9       | 52                | 59½                | 118                      | 3½          | 3350            | 0        |
| 46              | 10           | 52                | 47½                | 118                      | 0½          | 3560            | 0        |
| 47              | 11           | 53                | 3                  | 118                      | 6½          | 3340            | 0        |
| 48              | 12           | 53                | 5                  | 118                      | 3           | 3320            | 0        |
| 49              | 13           | 53                | 0                  | 118                      | 4½          | 3360            | 0        |
| 50              | 19           | 53                | 23                 | 118                      | 21          | 4500            | 0        |
| 51              | 23           | 52                | 33½                | 116                      | 53½         | 5100            | 0        |
| 52 <sup>1</sup> | June 14      | 52                | 59½                | 118                      | 4           | 3410            | N 60 E 2 |
| 53              | 14           | 52                | 59½                | 118                      | 4           | 3390            | S 40 E 1 |
| 54              | 15           | 52                | 59½                | 118                      | 4           | 3420            | 0        |
| 55              | 16           | 52                | 59½                | 118                      | 4           | 3410            | 0        |
| 56              | 17           | 52                | 59½                | 118                      | 4           | 3390            | S 70 E 3 |
| 57              | 18           | 52                | 59½                | 118                      | 4           | 3390            | 0        |
| 58 <sup>1</sup> | 22           | 49                | 5                  | 113                      | 51          | 4270            | 0        |
| 59              | 22           | 49                | 5                  | 113                      | 51          | 4270            | 0        |
| 60              | 24           | 49                | 5                  | 113                      | 51          | 4270            | 0        |
| 61              | 24           | 49                | 5                  | 113                      | 51          | 4270            | 0        |
| 62              | 26           | 49                | 5                  | 113                      | 51          | 4270            | 0        |
| 63              | 27           | 49                | 5                  | 113                      | 51          | 4270            | 0        |
| 64              | 21           | 49                | 6                  | 113                      | 53          | 4450            | S 2 W 6  |
| 65              | Aug. 2       | 49                | 5½                 | 113                      | 52½         | 4390            | S 50 E 4 |
| 66              | 7            | 49                | 5½                 | 113                      | 52½         | 4390            | S 25 E 1 |
| 67              | 8            | 49                | 5½                 | 113                      | 52½         | 4410            | S 25 E 5 |
| 68              | 13           | 49                | 5½                 | 113                      | 52½         | 4420            | S 35 W 6 |
| 69              | 14           | 49                | 5½                 | 113                      | 52½         | 4425            | S 20 W 1 |
| 70              | 15           | 49                | 5½                 | 113                      | 52½         | 4420            | N 25 W 5 |
| 71              | 15           | 49                | 5½                 | 113                      | 52½         | 4410            | N 5 E 3  |

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Footnotes: <sup>1</sup> - Stands 1 to 20, Waterton Lakes National Park, 1967.  
 Stands 21 to 35, Banff National Park, 1967.  
 Stands 36 to 51, Jasper National Park, 1967.  
 Stands 52 to 57, Jasper National Park, 1968.  
 Stands 58 to 71, Waterton Lakes National Park, 1968.

<sup>2</sup> - On the Ya-Ha Tinda Ranch, just outside the Banff National Park boundary.





APPENDIX 2. AERIAL PHOTOGRAPHS CORRESPONDING TO GRASSLAND  
AREAS IN BANFF, JASPER, AND WATERTON LAKES  
NATIONAL PARKS.

| Section No. | Roll or<br>Series No. | Flight Line | Photograph<br>Nos. |
|-------------|-----------------------|-------------|--------------------|
| 83 E 8      | 160                   | 5308X       | 26-28              |
| 83 F 4      | 160                   | 5305X       | 123                |
| 83 E 1      | 160                   | 5304XA      | 150                |
| 83 E 1      | 160                   | 5303X       | 22                 |
| 83 E 1      | 160                   | 5301X       | 18                 |
| 83 D 16     | 160                   | 5222X       | 71                 |
| 83 E 1      | 160                   | 5300X       | 16                 |
| 83 D 16     | 160                   | 5221X       | 15                 |
| 83 C 13     | 160                   | 5218X       | 12                 |
| 83 D 16     | 160                   | 5219X       | 10                 |
| 83 C 10     | 160                   | 5213X       | 30                 |
| 83 C 7      | 160                   | 5210X       | 142                |
| 82 O 12     | 160                   | 5116X       | 127-128            |
| 82 N 8      | 67-53                 | A20145      | 166-167            |
| 82 N 8      | 67-53                 | A20301      | 38-39              |
| 82 N 8      | 67-53                 | A20145      | 164-165            |
| 82 N 8      | 67-53                 | A20301      | 36-37              |
| 82 O 5      | 67-53                 | A20300      | 47-48              |
| 82 O 5      | 67-53                 | A20145      | 206                |
| 82 O 4      | 67-53                 | A20300      | 44                 |
| 82 O 4      | 67-53                 | A20145      | 202                |
| 82 O 4      | 67-53                 | A20300      | 35                 |
| 82 O 4      | 67-53                 | A20147      | 11-12              |
| 82 O 3      | 67-53                 | A20147      | 54-55              |
| 82 O 4      | 67-53                 | A20148      | 42                 |
| 82 O 3      | 67-53                 | A20147      | 53-54              |
| 82 O 4      | 67-53                 | A20148      | 41                 |
| 82 O 3      | 160                   | 5104X       | 18                 |
| 82 J 14     | 67-53                 | A20146      | 123                |
| 82 H 4      | YC 518                | 4905        | 33                 |
| 82 H 4      | YC 535                | 4904/5      | 5                  |
| 82 H 4      | YC 432                | 4904        | 144-145            |
| 82 H 4      | YC 432                | 4904        | 148-149            |
| 82 H 4      | YC 432                | 4902        | 87-88              |
| 82 H 4      | YC 432                | 4903        | 118-119            |
| 82 H 4      | YC 432                | 4902        | 92                 |
| 82 H 4      | YC 432                | 4902        | 93                 |
| 82 H 4      | YC 432                | 4901        | 60                 |



## APPENDIX 3. INDICES OF SIMILARITY STANDS.

| St. | 71 | 70 | 69 | 68 | 67 | 66 | 65 | 64 | 63 | 62 | 61 | 60 | 59 | 58 | 57 | 56 | 55 | 54 | 53 | 52 | 51 | 50 | 49 | 48 | 47 | 46 | 45 |
|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 1   | 46 | 51 | 47 | 44 | 45 | 54 | 52 | 50 | 46 | 33 | 8  | 20 | 23 | 33 | 21 | 9  | 16 | 19 | 15 | 17 | 22 | 19 | 9  | 5  | 5  | 11 | 11 |
| 2   | 39 | 38 | 41 | 43 | 41 | 47 | 40 | 40 | 37 | 30 | 16 | 41 | 44 | 49 | 23 | 18 | 19 | 22 | 21 | 26 | 16 | 19 | 16 | 14 | 22 | 14 | 23 |
| 3   | 47 | 46 | 41 | 41 | 44 | 48 | 49 | 42 | 40 | 31 | 8  | 20 | 27 | 34 | 23 | 10 | 25 | 24 | 11 | 16 | 16 | 24 | 11 | 8  | 9  | 7  | 14 |
| 4   | 40 | 50 | 50 | 53 | 54 | 47 | 50 | 52 | 46 | 42 | 3  | 14 | 24 | 33 | 33 | 16 | 29 | 31 | 19 | 20 | 13 | 15 | 14 | 11 | 8  | 6  | 15 |
| 5   | 29 | 40 | 45 | 48 | 46 | 41 | 44 | 45 | 40 | 45 | 12 | 24 | 26 | 38 | 22 | 12 | 16 | 23 | 24 | 31 | 18 | 10 | 17 | 18 | 17 | 5  | 25 |
| 6   | 44 | 60 | 61 | 57 | 64 | 58 | 58 | 60 | 50 | 40 | 7  | 20 | 22 | 34 | 16 | 8  | 11 | 14 | 11 | 13 | 16 | 10 | 6  | 4  | 7  | 8  | 16 |
| 7   | 32 | 63 | 61 | 68 | 69 | 50 | 59 | 66 | 53 | 53 | 6  | 18 | 25 | 34 | 19 | 15 | 11 | 13 | 14 | 18 | 18 | 10 | 17 | 10 | 13 | 5  | 14 |
| 8   | 32 | 59 | 51 | 65 | 62 | 51 | 56 | 62 | 45 | 44 | 5  | 17 | 28 | 37 | 27 | 19 | 15 | 21 | 21 | 26 | 20 | 10 | 22 | 15 | 16 | 7  | 20 |
| 9   | 31 | 18 | 16 | 15 | 17 | 24 | 13 | 17 | 12 | 9  | 34 | 64 | 35 | 27 | 8  | 1  | 9  | 8  | 9  | 12 | 19 | 17 | 8  | 3  | 5  | 17 | 14 |
| 10  | 14 | 8  | 5  | 4  | 5  | 11 | 3  | 4  | 6  | 3  | 61 | 35 | 18 | 14 | 0  | 0  | 3  | 2  | 2  | 5  | 10 | 11 | 2  | 2  | 4  | 11 | 5  |
| 11  | 36 | 38 | 36 | 34 | 35 | 39 | 35 | 38 | 31 | 23 | 19 | 45 | 40 | 36 | 18 | 12 | 14 | 17 | 19 | 21 | 15 | 21 | 9  | 8  | 12 | 14 | 19 |
| 12  | 49 | 47 | 46 | 45 | 48 | 58 | 49 | 51 | 41 | 32 | 10 | 26 | 33 | 43 | 18 | 13 | 15 | 16 | 14 | 24 | 18 | 19 | 16 | 15 | 18 | 13 | 14 |
| 13  | 32 | 49 | 49 | 54 | 54 | 47 | 57 | 54 | 42 | 50 | 7  | 24 | 35 | 40 | 36 | 29 | 22 | 28 | 28 | 38 | 21 | 17 | 27 | 26 | 29 | 9  | 26 |
| 14  | 44 | 44 | 45 | 40 | 45 | 52 | 49 | 49 | 33 | 23 | 14 | 33 | 32 | 37 | 17 | 11 | 14 | 18 | 14 | 15 | 16 | 17 | 11 | 9  | 8  | 6  | 15 |
| 15  | 49 | 46 | 43 | 38 | 43 | 55 | 48 | 46 | 37 | 26 | 12 | 32 | 38 | 46 | 18 | 11 | 17 | 19 | 11 | 15 | 17 | 22 | 13 | 7  | 10 | 18 | 17 |
| 16  | 46 | 54 | 50 | 41 | 47 | 56 | 50 | 48 | 33 | 19 | 15 | 27 | 29 | 33 | 18 | 10 | 16 | 18 | 14 | 15 | 21 | 17 | 9  | 6  | 6  | 10 | 11 |
| 17  | 40 | 38 | 35 | 35 | 37 | 46 | 38 | 42 | 34 | 25 | 8  | 36 | 52 | 50 | 21 | 16 | 15 | 18 | 14 | 20 | 15 | 17 | 16 | 16 | 11 | 14 | 18 |
| 18  | 51 | 67 | 62 | 60 | 65 | 59 | 65 | 66 | 49 | 40 | 5  | 21 | 30 | 35 | 24 | 12 | 19 | 20 | 14 | 16 | 15 | 13 | 12 | 8  | 8  | 6  | 15 |
| 19  | 34 | 58 | 66 | 68 | 67 | 54 | 59 | 62 | 50 | 40 | 7  | 21 | 25 | 38 | 23 | 13 | 13 | 18 | 15 | 19 | 20 | 10 | 13 | 7  | 10 | 8  | 16 |
| 20  | 48 | 58 | 65 | 60 | 60 | 65 | 58 | 61 | 43 | 35 | 9  | 28 | 30 | 42 | 21 | 11 | 14 | 17 | 15 | 19 | 21 | 17 | 12 | 11 | 6  | 8  | 11 |
| 21  | 26 | 25 | 20 | 25 | 22 | 30 | 24 | 26 | 22 | 21 | 5  | 23 | 36 | 36 | 29 | 21 | 26 | 30 | 29 | 27 | 38 | 31 | 24 | 14 | 21 | 25 | 33 |
| 22  | 22 | 9  | 3  | 3  | 8  | 23 | 4  | 8  | 6  | 1  | 11 | 28 | 27 | 22 | 1  | 1  | 6  | 4  | 2  | 5  | 13 | 21 | 6  | 0  | 2  | 21 | 7  |
| 23  | 20 | 14 | 15 | 11 | 14 | 17 | 11 | 13 | 10 | 8  | 4  | 12 | 15 | 11 | 21 | 9  | 31 | 25 | 13 | 9  | 24 | 38 | 5  | 5  | 6  | 7  | 9  |
| 24  | 12 | 6  | 8  | 7  | 5  | 6  | 6  | 5  | 6  | 5  | 5  | 14 | 10 | 8  | 16 | 2  | 25 | 16 | 7  | 5  | 11 | 19 | 3  | 3  | 3  | 6  | 4  |
| 25  | 20 | 12 | 12 | 10 | 11 | 18 | 11 | 11 | 9  | 9  | 13 | 19 | 21 | 13 | 10 | 6  | 7  | 10 | 9  | 12 | 10 | 43 | 7  | 10 | 11 | 7  | 8  |
| 26  | 29 | 14 | 16 | 13 | 11 | 18 | 12 | 12 | 13 | 10 | 6  | 19 | 20 | 19 | 26 | 8  | 29 | 25 | 12 | 11 | 15 | 25 | 6  | 9  | 7  | 11 | 17 |
| 27  | 20 | 20 | 21 | 22 | 20 | 23 | 20 | 19 | 21 | 23 | 12 | 26 | 27 | 30 | 29 | 21 | 22 | 27 | 21 | 24 | 31 | 25 | 20 | 15 | 31 | 13 | 30 |
| 28  | 27 | 33 | 30 | 34 | 35 | 30 | 29 | 32 | 31 | 31 | 5  | 17 | 20 | 26 | 35 | 24 | 29 | 33 | 29 | 28 | 32 | 35 | 27 | 12 | 23 | 11 | 30 |
| 29  | 28 | 35 | 29 | 36 | 36 | 35 | 35 | 36 | 31 | 29 | 7  | 15 | 19 | 21 | 22 | 10 | 15 | 18 | 18 | 15 | 30 | 22 | 17 | 7  | 15 | 13 | 25 |
| 30  | 20 | 24 | 18 | 23 | 20 | 23 | 19 | 19 | 19 | 21 | 7  | 23 | 31 | 34 | 28 | 29 | 19 | 29 | 29 | 29 | 36 | 29 | 30 | 20 | 27 | 25 | 34 |
| 31  | 15 | 26 | 26 | 29 | 28 | 22 | 26 | 28 | 24 | 21 | 3  | 13 | 17 | 28 | 25 | 26 | 27 | 32 | 22 | 42 | 25 | 31 | 13 | 28 | 14 | 31 |    |
| 32  | 33 | 29 | 26 | 28 | 28 | 34 | 32 | 26 | 26 | 25 | 5  | 14 | 18 | 27 | 49 | 33 | 38 | 48 | 47 | 34 | 38 | 33 | 41 | 25 | 40 | 14 | 50 |
| 33  | 27 | 22 | 21 | 24 | 23 | 31 | 22 | 21 | 22 | 21 | 7  | 28 | 33 | 36 | 20 | 21 | 20 | 26 | 24 | 20 | 25 | 25 | 24 | 13 | 20 | 18 | 28 |
| 34  | 29 | 21 | 17 | 14 | 18 | 33 | 20 | 21 | 17 | 9  | 14 | 26 | 30 | 27 | 11 | 3  | 14 | 13 | 9  | 9  | 20 | 40 | 4  | 0  | 5  | 16 | 10 |
| 35  | 14 | 21 | 24 | 26 | 22 | 17 | 20 | 18 | 20 | 27 | 5  | 15 | 18 | 19 | 48 | 50 | 27 | 43 | 58 | 48 | 31 | 14 | 66 | 48 | 65 | 9  | 59 |
| 36  | 12 | 16 | 13 | 16 | 17 | 13 | 16 | 13 | 15 | 21 | 3  | 7  | 10 | 19 | 44 | 55 | 34 | 41 | 37 | 45 | 27 | 11 | 63 | 53 | 59 | 12 | 41 |

| 44 | 43 | 42 | 41 | 40 | 39 | 38 | 37 | 36 | 35 | 34 | 33 | 32 | 31 | 30 | 29 | 28 | 27 | 26 | 25 | 24 | 23 | 22 | 21 | 20 | 19 |
|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 13 | 8  | 19 | 14 | 13 | 13 | 18 | 2  | 13 | 18 | 24 | 22 | 30 | 22 | 19 | 29 | 24 | 20 | 18 | 19 | 11 | 20 | 11 | 28 | 54 | 48 |
| 28 | 15 | 30 | 26 | 16 | 29 | 25 | 14 | 21 | 29 | 18 | 30 | 25 | 25 | 35 | 21 | 29 | 38 | 24 | 19 | 9  | 12 | 18 | 40 | 43 | 42 |
| 16 | 10 | 17 | 14 | 9  | 13 | 17 | 6  | 16 | 17 | 23 | 32 | 34 | 23 | 22 | 22 | 29 | 25 | 16 | 14 | 13 | 25 | 15 | 31 | 42 | 37 |
| 15 | 14 | 22 | 13 | 6  | 12 | 18 | 10 | 14 | 23 | 12 | 22 | 31 | 22 | 14 | 32 | 28 | 26 | 15 | 8  | 9  | 16 | 4  | 22 | 51 | 47 |
| 21 | 10 | 20 | 15 | 6  | 23 | 18 | 13 | 20 | 24 | 13 | 26 | 27 | 20 | 20 | 25 | 28 | 29 | 16 | 15 | 9  | 11 | 6  | 26 | 38 | 43 |
| 14 | 9  | 18 | 13 | 8  | 12 | 18 | 3  | 10 | 19 | 16 | 20 | 27 | 17 | 21 | 25 | 27 | 19 | 13 | 8  | 3  | 11 | 6  | 20 | 60 | 60 |
| 13 | 13 | 21 | 11 | 7  | 13 | 17 | 10 | 20 | 24 | 12 | 18 | 20 | 28 | 21 | 32 | 34 | 20 | 9  | 9  | 4  | 10 | 4  | 21 | 56 | 59 |
| 17 | 19 | 25 | 14 | 6  | 19 | 23 | 12 | 24 | 28 | 13 | 16 | 27 | 24 | 21 | 29 | 29 | 24 | 14 | 12 | 7  | 13 | 4  | 24 | 60 | 58 |
| 28 | 4  | 15 | 19 | 19 | 9  | 9  | 3  | 10 | 12 | 22 | 26 | 13 | 11 | 19 | 12 | 16 | 23 | 16 | 14 | 11 | 9  | 29 | 21 | 21 | 20 |
| 12 | 0  | 6  | 15 | 8  | 6  | 1  | 0  | 5  | 4  | 14 | 9  | 5  | 3  | 9  | 7  | 7  | 15 | 6  | 8  | 6  | 6  | 17 | 8  | 8  | 8  |
| 27 | 10 | 25 | 23 | 14 | 18 | 20 | 6  | 14 | 20 | 25 | 25 | 20 | 18 | 25 | 22 | 23 | 31 | 26 | 16 | 10 | 14 | 13 | 30 | 36 | 29 |
| 19 | 13 | 24 | 14 | 9  | 15 | 17 | 11 | 18 | 20 | 26 | 26 | 29 | 21 | 21 | 22 | 23 | 21 | 18 | 13 | 9  | 13 | 12 | 27 | 50 | 40 |
| 30 | 26 | 34 | 16 | 10 | 30 | 23 | 21 | 29 | 39 | 15 | 26 | 37 | 34 | 30 | 28 | 34 | 35 | 19 | 18 | 8  | 12 | 5  | 36 | 49 | 50 |
| 15 | 9  | 20 | 11 | 8  | 19 | 17 | 5  | 15 | 16 | 21 | 16 | 28 | 18 | 19 | 20 | 20 | 22 | 20 | 17 | 15 | 21 | 10 | 21 | 60 | 48 |
| 26 | 12 | 21 | 17 | 19 | 14 | 19 | 6  | 15 | 14 | 27 | 32 | 30 | 23 | 28 | 27 | 26 | 30 | 20 | 13 | 11 | 15 | 21 | 33 | 49 | 39 |
| 15 | 7  | 19 | 12 | 19 | 15 | 18 | 13 | 12 | 16 | 27 | 19 | 27 | 19 | 23 | 26 | 21 | 19 | 21 | 16 | 14 | 15 | 13 | 22 | 60 | 40 |
| 25 | 16 | 24 | 19 | 16 | 13 | 20 | 15 | 17 | 21 | 20 | 27 | 31 | 20 | 30 | 16 | 18 | 23 | 24 | 12 | 8  | 10 | 15 | 34 | 43 | 31 |
| 19 | 13 | 23 | 12 | 6  | 9  | 20 | 8  | 11 | 18 | 20 | 21 | 31 | 21 | 13 | 33 | 33 | 23 | 19 | 11 | 12 | 14 | 8  | 21 | 65 | 59 |
| 19 | 14 | 20 | 12 | 7  | 14 | 19 | 8  | 16 | 18 | 13 | 17 | 23 | 31 | 20 | 27 | 32 | 23 | 14 | 11 | 10 | 10 | 8  | 24 | 66 |    |
| 15 | 10 | 23 | 12 | 7  | 14 | 17 | 8  | 14 | 21 | 23 | 19 | 29 | 25 | 23 | 32 | 28 | 25 | 18 | 14 | 9  | 17 | 7  | 26 |    |    |
| 35 | 23 | 30 | 37 | 30 | 28 | 25 | 15 | 28 | 29 | 25 | 48 | 41 | 59 | 64 | 30 | 42 | 42 | 17 | 19 | 6  | 26 | 27 |    |    |    |
| 24 | 1  | 6  | 18 | 37 | 7  | 3  | 0  | 6  | 2  | 38 | 41 | 18 | 17 | 24 | 17 | 24 | 16 | 11 | 22 | 6  | 17 |    |    |    |    |
| 16 | 6  | 11 | 13 | 9  | 8  | 11 | 1  | 7  | 7  | 35 | 27 | 20 | 30 | 15 | 15 | 25 | 22 | 26 | 36 | 25 |    |    |    |    |    |
| 19 | 4  | 11 | 7  | 6  | 4  | 11 | 3  | 5  | 6  | 16 | 8  | 11 | 10 | 6  | 5  | 11 | 8  | 46 | 21 |    |    |    |    |    |    |
| 8  | 5  | 9  | 9  | 8  | 14 | 8  | 5  | 8  | 12 | 35 | 18 | 18 | 13 | 15 | 19 | 21 | 18 | 22 |    |    |    |    |    |    |    |
| 25 | 8  | 19 | 15 | 13 | 13 | 18 | 8  | 10 | 15 | 24 | 16 | 21 | 17 | 15 | 13 | 16 | 19 |    |    |    |    |    |    |    |    |
| 34 | 21 | 29 | 32 | 14 | 32 | 27 | 17 | 24 | 37 | 20 | 40 | 45 | 37 | 36 | 32 | 49 |    |    |    |    |    |    |    |    |    |
| 32 | 24 | 31 | 29 | 16 | 27 | 28 | 10 | 28 | 32 | 32 | 39 | 52 | 40 | 36 | 45 |    |    |    |    |    |    |    |    |    |    |
| 20 | 14 | 22 | 20 | 11 | 20 | 26 | 4  | 18 | 27 | 27 | 28 | 39 | 24 | 26 |    |    |    |    |    |    |    |    |    |    |    |
| 33 | 29 | 35 | 39 | 26 | 31 | 25 | 20 | 31 | 35 | 21 | 45 | 40 | 55 |    |    |    |    |    |    |    |    |    |    |    |    |
| 33 | 28 | 34 | 34 | 19 | 30 | 30 | 15 | 31 | 30 | 19 | 44 | 40 |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 46 | 41 | 49 | 41 | 18 | 39 | 48 | 26 | 43 | 52 | 25 | 44 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 36 | 22 | 27 | 33 | 28 | 22 | 23 | 17 | 23 | 25 | 33 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 20 | 3  | 19 | 24 | 17 | 10 | 13 | 0  | 7  | 10 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 42 | 66 | 62 | 22 | 9  | 48 | 45 | 37 | 49 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 36 | 56 | 56 | 31 | 12 | 58 | 43 | 62 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |



| St. | 71 | 70 | 69 | 68 | 67 | 66 | 65 | 64 | 63 | 62 | 61 | 60 | 59 | 58 | 57 | 56 | 55 | 54 | 53 | 52 | 51 | 50 | 49 | 48 | 47 | 46 | 45 | 44 | 43 | 42 | 41 | 40 | 39 | 38 |
|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 37  | 3  | 10 | 8  | 11 | 10 | 5  | 9  | 7  | 11 | 18 | 0  | 4  | 9  | 13 | 34 | 53 | 23 | 26 | 24 | 35 | 8  | 6  | 50 | 62 | 44 | 1  | 24 | 22 | 50 | 41 | 18 | 1  | 30 | 26 |
| 38  | 17 | 21 | 18 | 25 | 20 | 16 | 22 | 19 | 16 | 16 | 4  | 11 | 14 | 16 | 55 | 40 | 43 | 49 | 52 | 36 | 39 | 16 | 44 | 23 | 45 | 8  | 57 | 47 | 52 | 64 | 26 | 7  | 43 |    |
| 39  | 12 | 14 | 11 | 16 | 14 | 15 | 13 | 11 | 12 | 19 | 4  | 11 | 14 | 19 | 34 | 36 | 27 | 35 | 44 | 33 | 27 | 12 | 48 | 31 | 58 | 8  | 53 | 43 | 43 | 49 | 25 | 7  |    |    |
| 40  | 16 | 7  | 5  | 6  | 5  | 14 | 6  | 5  | 7  | 8  | 4  | 19 | 22 | 16 | 8  | 5  | 16 | 15 | 11 | 4  | 21 | 22 | 7  | 1  | 5  | 56 | 14 | 27 | 7  | 15 | 35 |    |    |    |
| 41  | 13 | 16 | 8  | 16 | 15 | 19 | 17 | 16 | 17 | 16 | 10 | 18 | 17 | 21 | 16 | 24 | 21 | 24 | 29 | 17 | 24 | 24 | 23 | 14 | 23 | 37 | 31 | 33 | 25 | 34 |    |    |    |    |
| 42  | 18 | 25 | 22 | 27 | 21 | 19 | 23 | 19 | 18 | 24 | 7  | 16 | 21 | 21 | 54 | 54 | 40 | 50 | 60 | 51 | 33 | 21 | 64 | 41 | 60 | 16 | 54 | 53 | 68 |    |    |    |    |    |
| 43  | 8  | 16 | 14 | 20 | 14 | 10 | 14 | 12 | 15 | 23 | 2  | 3  | 9  | 13 | 50 | 71 | 33 | 45 | 60 | 53 | 20 | 12 | 83 | 49 | 58 | 10 | 66 | 40 |    |    |    |    |    |    |
| 44  | 18 | 15 | 14 | 17 | 13 | 16 | 14 | 14 | 12 | 17 | 6  | 26 | 24 | 23 | 44 | 35 | 39 | 44 | 43 | 37 | 38 | 23 | 38 | 22 | 49 | 23 | 53 |    |    |    |    |    |    |    |
| 45  | 14 | 16 | 17 | 22 | 18 | 15 | 16 | 14 | 15 | 22 | 4  | 12 | 15 | 17 | 46 | 48 | 30 | 44 | 61 | 47 | 33 | 18 | 61 | 30 | 53 | 16 |    |    |    |    |    |    |    |    |
| 46  | 15 | 10 | 7  | 7  | 7  | 16 | 8  | 8  | 7  | 6  | 6  | 14 | 16 | 13 | 7  | 7  | 12 | 13 | 11 | 8  | 21 | 18 | 9  | 5  | 8  |    |    |    |    |    |    |    |    |    |
| 47  | 6  | 11 | 9  | 13 | 10 | 6  | 10 | 6  | 11 | 18 | 2  | 7  | 10 | 16 | 41 | 50 | 24 | 36 | 44 | 40 | 26 | 11 | 62 | 50 |    |    |    |    |    |    |    |    |    |    |
| 48  | 6  | 11 | 12 | 11 | 10 | 7  | 11 | 8  | 11 | 21 | 0  | 6  | 11 | 15 | 36 | 45 | 21 | 30 | 31 | 42 | 11 | 7  | 58 |    |    |    |    |    |    |    |    |    |    |    |
| 49  | 10 | 15 | 16 | 18 | 18 | 10 | 15 | 14 | 16 | 24 | 2  | 6  | 9  | 15 | 46 | 67 | 34 | 45 | 61 | 61 | 24 | 11 |    |    |    |    |    |    |    |    |    |    |    |    |
| 50  | 28 | 14 | 12 | 11 | 10 | 24 | 12 | 12 | 10 | 9  | 11 | 21 | 22 | 15 | 29 | 12 | 25 | 32 | 17 | 15 | 26 |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 51  | 18 | 18 | 13 | 16 | 16 | 19 | 15 | 17 | 8  | 9  | 7  | 14 | 13 | 13 | 32 | 17 | 29 | 31 | 31 | 26 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 52  | 14 | 21 | 22 | 22 | 19 | 17 | 21 | 20 | 14 | 27 | 6  | 12 | 13 | 17 | 54 | 65 | 37 | 51 | 64 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 53  | 13 | 16 | 17 | 19 | 15 | 12 | 15 | 13 | 12 | 19 | 4  | 9  | 12 | 11 | 55 | 54 | 44 | 59 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 54  | 21 | 18 | 20 | 21 | 17 | 17 | 18 | 16 | 15 | 24 | 5  | 10 | 14 | 16 | 80 | 50 | 74 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 55  | 19 | 12 | 13 | 15 | 12 | 13 | 12 | 10 | 12 | 18 | 4  | 8  | 10 | 8  | 69 | 38 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 56  | 9  | 17 | 16 | 18 | 16 | 11 | 13 | 11 | 15 | 22 | 2  | 3  | 11 | 13 | 50 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 57  | 21 | 23 | 23 | 26 | 21 | 17 | 21 | 18 | 16 | 25 | 3  | 9  | 13 | 17 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 58  | 38 | 38 | 35 | 41 | 38 | 46 | 39 | 42 | 47 | 32 | 10 | 40 | 66 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 59  | 36 | 28 | 23 | 27 | 23 | 39 | 28 | 32 | 35 | 24 | 13 | 52 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 60  | 38 | 22 | 18 | 20 | 20 | 32 | 21 | 25 | 24 | 15 | 35 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 61  | 12 | 9  | 7  | 5  | 6  | 10 | 5  | 5  | 5  | 4  |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 62  | 23 | 46 | 46 | 57 | 50 | 32 | 49 | 47 | 62 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 63  | 35 | 56 | 51 | 64 | 62 | 48 | 62 | 65 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 64  | 42 | 69 | 67 | 68 | 72 | 62 | 76 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 65  | 44 | 70 | 70 | 72 | 77 | 62 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 66  | 63 | 67 | 59 | 59 | 63 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 67  | 44 | 78 | 79 | 81 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 68  | 35 | 69 | 77 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 69  | 43 | 72 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 70  | 54 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 71  |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |





in the order found in MOSS (1959) "Flora of Alberta"; the genus *Agropyron* according to Bowden (1965). abundance values less than 1 are listed below this table.

WATERTON LAKES N.P., 1968.

[illegible]









[illegible]



[illegible]



[illegible]





[illegible]



Other species recorded were as follows: Ophioglossaceae, *Botrychium lunaria* (L.) SW. (Stand *Alopecurus occidentalis* Scribn. & Tweedy (No. 61=P), *Agrostis scabra* Willd. (No. 1=P, No. 12=P), *Pheum alpinum* L. (No. 25=+), *Poa ampla* Merr. (No. 29=+, No. 66=P), *Poa glauca* Vahl (No. 38=+), *Pitche*. (No. 12=P), *Trisetum spicatum* (L.) Richt. (No. 25=+, No. 50=+); Cyperaceae, *Carex aene* *Carex drummondiana* Dewey (No. 8=P), *Carex hoodii* Boott (No. 4=P, No. 24=P), *Carex interior* Bai (No. 10=P, No. 61=+), *Juncus tenuis* Willd. var. *dudleyi* (Wieg.) Hermann (No. 61=P); Liliaceae, (No. 62=+), *Polygonum bistortoides* Pursh (No. 16=P), *Polygonum viviparum* L. (No. 23=P); Rumex L. var. *hirsutum* Fries (No. 10=P, No. 61=+); Ranunculaceae, *Anemone cylindrica* A. Gray (No. 12, No. 61=P); Fumariaceae, *Corydalis aurea* Willd. (No. 26=P); Cruciferae, *Arabis hirsuta* (L.) Scop. *Draba praealta* Greene (No. 23=+), *Erucastrum gallicum* (Willd.) Schulz (No. 39=P), *Sisymbrium pseudorupestris* (Rydb.) Keck (No. 4=P), *Potentilla norvegica* L. (No. 39=P, No. 46=+), *Prunus vir* (Hook.) S. Wats. (No. 25=+), *Astragalus missouriensis* Nutt. (No. 13=P), *Hedysarum boreale* Nutt. & Trautv. (No. 26=+); Violaceae, *Viola nuttallii* Pursh (No. 2=P); Umbelliferae, *Heracleum lan* *Mathias* (No. 2=P), *Perideridia gairdneri* (Hook. & Arn.) Mathias (No. 14=P, No. 20=+); Gentianaceae hydrophyllaceae, *Phacelia heterophylla* Pursh (No. 3=P, No. 4=P); Boraginaceae, *Lappula echinat* *Euphrasia disjuncta* Fern. & Wieg. (No. 51=+), *Penstemon virens* Pennell (No. 4=+); Compositae, (No. 2=P, No. 4=P), *Artemisia mitchauriana* Bess. (No. 4=P), *Crepis atrabarba* Heller (No. 6=+, No. =P), *Lactuca pulchella* (Pursh) DC. (No. 21=P, No. 37=P), *Liatriis punctata* Hook. (No. 7=+, No. 67 =P); Polypodiaceae, *Cystopteris fragilis* (L.) Bernh. (No. 4=+); Juncaginaceae, *Triglochin* (No. 66=+), *Bromus ciliatus* L. (No. 40=P), *Bromus marginatus* Nees (No. 15=+, No. 66=P), *Calamagrost* *Poa nervosa* (Hook.) Vasey (No. 23=P), *Poa rupicola* Nash (No. 21=P), *Schizachne purpurascens* (To a Fern. (No. 40=+, No. 41=P), *Carex atosquama* Mack. (No. 25=+), *Carex aurea* Nutt. (No. 10=P, No. 60=+ ley (No. 10=+, No. 61=+), *Carex media* R.Br. (No. 25=+), *Carex umbellata* Schk. (No. 21=+, No. 35=P), *Lilium philadelphicum* L. var. *andinum* (Nutt.) Ker (No. 10=P, No. 63=+); Orchidaceae, *Habenaria aspestris* (Scop.) Löve (No. 60=P); Caryophyllaceae, *Arenaria obtusiloba* (Rydb.) Fern. (No. 7=+, =P, No. 71=+), *Anemone parviflora* Michx. (No. 23=P), *Clematis verticellaris* D.C. var. *columbiana* (No. 26=P), *Braya richardsonii* (Rydb.) Fern. (No. 36=P, No. 37=P, No. 48=+), *Draba aurea* Vahl (No. 16 altissimum L. (No. 4=P); Saxifragaceae, *Ribes oxyacanthoides* L. (No. 40=P, No. 51=P); Rosaceae, *gniana* L. (No. 4=P, No. 8=+, No. 14=P); Leguminosae, *Astragalus aboriginum* Richards (No. 2=P, No. 5=+, (No. 62=P), *Hedysarum mackenzii* Richards (No. 39=P, No. 44=+), *Oxytropis viscida* Nutt. (No. 23=P), *atum* Michx. (No. 24=+), *Lomatium dissectum* (Nutt.) Mathias & Constance var. *multifidum* (Nutt.) e, *Gentianella propinqua* (Richards.) J.M. Gillett (No. 51=+); Apocynaceae, *Apocynum androsaemif* a (No. 39=P, No. 41=P, No. 47=P); Labiatae, *Prunella vulgaris* L. (No. 61=+); Scrophulariaceae, *Besse* *Antennaria lanata* (Hook.) Greene (No. 23=P), *Antennaria neglecta* Greene (No. 1=+), *Antennaria* 19=+, No. 67=+), *Crepis runcinata* (James) T. & G. (No. 30=+, No. 61=+), *Erigeron lonchophyllus* Hook. =P), *Taraxacum laevigatum* (Willd.) DC. No. 1=+).





Species listed quantitatively by Cover-abundance values;  
Species with Presence Values of less than 5% and Cover-

nomenclature follows BIRD (1966) for lichens and BIRD (1968) for Mosses.  
abundance values less than 1 are listed below this table.

WATERTON LAKES N.P., 1967.

BANFF N.P., 1967

JASPER N. P., 1967.

JASPER N.P., 1968.

WATERTON LAKES N.P., 1968.

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## WATERTON LAKES N.P., 1967.

Other species recorded were as follows: MOSSES; Encalyptaceae, *Encalypta vulgaris* Hedw., (Stand No. 38=P); Pottiaceae, *Tortella tortuosa* (Hedw.) Limpr. (No. 31=P, No. 54=P, No. 70=+ ); *Tortula ruraliformis* (Besch.) Dix. (No. 70 = +); Bryaceae, *Pohlia nutans* (Hedw.) Lindb. (No. 54=P); Mniaceae, *Mnium affine* Bland. Ex Funck (No. 10=+), *Mnium marginatum* (W. Hedw. (No. 3=+), *Hypnum revolutum* (Mitt.) Lindb. (No. 32=+), *Pylaisiella polyantha* (Hedw.) Grout (No. 55=P); Rhytidiaceae, *Rhytidium rugosum* (Hedw.) Kindb. (No. 55=P). LICHENS; Peltigeraceae, *Peltigera aphthosa* (L.) Willd. (No. 23=P, No. 25=+); Lecanoraceae, *Lecanora epibryon* (Ach.) Ach. (No. 30=+); Parmeliaceae, *Parmelia sulcata* Tayl. (No. 69=P); Physciaceae, *Pinodina* sp. (No. 49=+, No. 55=P); Teloschistaceae, *Caloplaca jungermanniae* (Vahl) Th.Fr. (No. 49=+); *Caloplaca stillacidiorum* (Vahl) Lynge (No. 27=P).

1881

1881

1881

1881

1881

## APPENDIX 6. LOCATIONS OF STANDS ON THE 51-STAND ORDINATION (1967).

| Stand | X axis <sup>1</sup> | Y axis <sup>2</sup> | Z axis <sup>3</sup> |
|-------|---------------------|---------------------|---------------------|
| 1     | 24.1                | 40.1                | 14.7                |
| 2     | 24.8                | 25.2                | 23.2                |
| 3     | 29.1                | 39.5                | 15.6                |
| 4     | 13.1                | 42.6                | 28.1                |
| 5     | 11.7                | 37.6                | 35.0                |
| 6     | 16.6                | 31.0                | 10.3                |
| 7     | 9.0                 | 31.5                | 24.2                |
| 8     | 9.0                 | 34.7                | 31.0                |
| 9     | 54.7                | 40.1                | 22.7                |
| 10    | 56.1                | 44.5                | 35.0                |
| 11    | 26.9                | 33.4                | 15.3                |
| 12    | 21.5                | 35.6                | 23.2                |
| 13    | 0                   | 28.2                | 34.3                |
| 14    | 21.0                | 43.1                | 14.9                |
| 15    | 31.3                | 33.1                | 0                   |
| 16    | 23.5                | 39.7                | 9.4                 |
| 17    | 23.1                | 28.5                | 24.2                |
| 18    | 11.6                | 46.6                | 15.1                |
| 19    | 15.6                | 38.3                | 20.7                |
| 20    | 15.0                | 34.8                | 18.5                |
| 21    | 41.0                | 6.7                 | 31.5                |
| 22    | 94.6                | 30.4                | 26.5                |
| 23    | 51.9                | 55.2                | 37.2                |
| 24    | 45.1                | 94.2                | 38.7                |
| 25    | 50.4                | 52.1                | 43.7                |
| 26    | 40.3                | 69.6                | 36.2                |
| 27    | 32.3                | 23.8                | 34.5                |
| 28    | 40.0                | 26.8                | 34.3                |
| 29    | 38.4                | 28.6                | 28.5                |
| 30    | 42.9                | 0                   | 40.3                |
| 31    | 33.7                | 14.8                | 38.5                |
| 32    | 33.2                | 24.1                | 42.8                |
| 33    | 57.7                | 18.3                | 30.8                |
| 34    | 65.2                | 43.5                | 22.5                |
| 35    | 16.3                | 22.0                | 71.7                |
| 36    | 27.3                | 23.9                | 74.0                |
| 37    | 27.4                | 30.7                | 86.5                |
| 38    | 28.8                | 35.0                | 50.3                |
| 39    | 27.9                | 23.5                | 60.3                |
| 40    | 68.7                | 29.0                | 28.9                |
| 41    | 48.6                | 21.1                | 43.9                |
| 42    | 23.6                | 27.1                | 61.4                |
| 43    | 24.4                | 24.4                | 74.1                |





## APPENDIX 6. Cont'd.

| Stand | X axis <sup>1</sup> | Y axis <sup>2</sup> | Z axis <sup>3</sup> |
|-------|---------------------|---------------------|---------------------|
| 44    | 43.0                | 36.8                | 43.6                |
| 45    | 30.7                | 21.4                | 56.6                |
| 46    | 57.5                | 29.8                | 34.3                |
| 47    | 23.1                | 25.8                | 76.5                |
| 48    | 23.6                | 31.5                | 93.3                |
| 49    | 28.4                | 22.8                | 78.2                |
| 50    | 50.9                | 39.4                | 33.1                |
| 51    | 40.1                | 26.7                | 40.7                |

Footnotes: <sup>1</sup> - Distance along X axis from stand #13.

<sup>2</sup> - Distance along Y axis from stand #30.

<sup>3</sup> - Distance along Z axis from stand #15.



APPENDIX 7. LOCATIONS OF 20 INTENSIVE STUDY SITE STANDS (1968)  
ON THE 51-STAND ORDINATION (1967).

| Stand           | X axis <sup>1</sup> | Y axis <sup>2</sup> | Z axis <sup>3</sup> |
|-----------------|---------------------|---------------------|---------------------|
| 52 <sup>4</sup> | 20.2                | 25.7                | 66.9                |
| 53              | 24.4                | 27.6                | 63.2                |
| 54              | 26.7                | 37.0                | 55.9                |
| 55              | 33.1                | 52.3                | 50.4                |
| 56              | 22.4                | 23.7                | 72.5                |
| 57              | 17.5                | 37.7                | 60.8                |
| 58 <sup>5</sup> | 33.7                | 24.8                | 23.4                |
| 59              | 41.6                | 29.8                | 24.8                |
| 60              | 50.0                | 39.2                | 23.9                |
| 61              | 51.9                | 45.8                | 34.9                |
| 62              | 9.3                 | 32.4                | 42.7                |
| 63              | 17.7                | 35.5                | 25.9                |
| 64 <sup>6</sup> | 13.3                | 34.1                | 17.3                |
| 65              | 7.6                 | 35.4                | 19.2                |
| 66              | 31.0                | 31.6                | 11.1                |
| 67              | 14.7                | 33.6                | 20.3                |
| 68              | 8.6                 | 32.5                | 25.1                |
| 69              | 11.9                | 38.1                | 22.8                |
| 70              | 17.5                | 30.5                | 20.1                |
| 71              | 39.6                | 40.1                | 13.1                |

- Footnotes:
- <sup>1</sup> - Distance along X axis from stand No. 13.
  - <sup>2</sup> - Distance along Y axis from stand No. 30.
  - <sup>3</sup> - Distance along Z axis from stand No. 15.
  - <sup>4</sup> - Stands 52-57; Henry House Intensive Study Site, Jasper National Park.
  - <sup>5</sup> - Stands 58-63; Hay Meadow Intensive Study Site, Waterton Lakes National Park.
  - <sup>6</sup> - Stands 64-71; Badlands Intensive Study Site, Waterton Lakes National Park.





APPENDIX 8. LOCATIONS OF STANDS ON THE 30-STAND *FESTUCA-DANTHONIA* PRAIRIE ORDINATION.

| Stand | X axis <sup>1</sup> | Y axis <sup>2</sup> | Z axis <sup>3</sup> |
|-------|---------------------|---------------------|---------------------|
| 1     | 19.3                | 29.9                | 0.0                 |
| 2     | 40.9                | 34.7                | 24.0                |
| 3     | 24.3                | 34.7                | 17.1                |
| 4     | 14.1                | 47.7                | 42.2                |
| 5     | 21.7                | 48.8                | 23.9                |
| 6     | 7.1                 | 33.9                | 29.2                |
| 7     | 7.9                 | 48.5                | 47.8                |
| 8     | 14.5                | 41.4                | 42.6                |
| 11    | 42.1                | 24.8                | 36.2                |
| 12    | 26.6                | 30.2                | 30.6                |
| 13    | 24.9                | 44.5                | 43.5                |
| 14    | 28.4                | 10.0                | 37.2                |
| 15    | 34.2                | 18.0                | 31.3                |
| 16    | 23.5                | 0.0                 | 32.0                |
| 17    | 49.2                | 23.8                | 43.7                |
| 18    | 14.5                | 32.0                | 53.7                |
| 19    | 8.9                 | 41.1                | 36.9                |
| 20    | 17.1                | 24.5                | 34.9                |
| 58    | 55.5                | 39.6                | 29.6                |
| 59    | 76.8                | 36.1                | 36.0                |
| 62    | 16.6                | 81.3                | 35.1                |
| 63    | 20.3                | 59.1                | 30.1                |
| 64    | 12.9                | 39.6                | 39.3                |
| 65    | 7.8                 | 40.1                | 37.0                |
| 66    | 23.3                | 24.1                | 31.1                |
| 67    | 0.0                 | 42.6                | 43.0                |
| 68    | 6.3                 | 51.1                | 40.5                |
| 69    | 2.6                 | 38.5                | 39.6                |
| 70    | 8.2                 | 35.4                | 38.8                |
| 71    | 32.0                | 21.7                | 32.0                |

Footnotes: <sup>1</sup>- Distance along X axis from stand No. 67.

<sup>2</sup>- Distance along Y axis from stand No. 16.

<sup>3</sup>- Distance along Z axis from stand No. 1.



## APPENDIX 9. PHYSICAL AND CHEMICAL PROPERTIES OF THE SOIL HORIZONS.

| Stand | Horizon<br>(cm)   | Munsell <sup>1,2</sup><br>colour | Gravel<br>% | Texture, <sup>3,2</sup><br>Sand Silt Clay | Text. <sup>2,3</sup><br>class | Moisture<br>FC | Char., <sup>2,4</sup><br>PWP AW | Avail. Nutrients, ppm. <sup>2,5</sup><br>N P K | pH <sup>2</sup> | Free <sup>2,6</sup><br>Lime | Inorg. <sup>2,7</sup><br>% | Organic <sup>2,7</sup><br>% |
|-------|-------------------|----------------------------------|-------------|-------------------------------------------|-------------------------------|----------------|---------------------------------|------------------------------------------------|-----------------|-----------------------------|----------------------------|-----------------------------|
| 1     | 0-10              | 5 yr 3.5/2                       | 47.0        | 67.0 29.9 3.1                             | SaL                           | 24.0           | 15.1 8.9                        | 14½ 7½ 165                                     | 6.2             | O                           |                            |                             |
|       | 10-20             | 5 yr 4.5/2                       | 29.3        | 67.3 27.8 4.9                             | SaL                           | 18.3           | 6.9 11.4                        | 6 2½ 64                                        | 6.2             | O                           |                            |                             |
|       | 20-71             | 5 yr 6/3                         | 29.0        | 56.9 30.6 12.5                            | SaL                           | 17.0           | 5.3 11.7                        | ½ 1 33                                         | 6.3             | O                           |                            |                             |
| 2     | 0-10 <sup>8</sup> |                                  | 0.3         | 87.1 9.0 3.9                              | Sa                            | 9.7            | 4.8 4.9                         | 1½ 3½ 131                                      | 7.5             | L                           |                            |                             |
|       | 10-33             | 7.5 yr 5/1                       | 3.3         | 83.0 13.6 3.4                             | LSa                           | 11.0           | 5.7 5.3                         | 2 2½ 84                                        | 7.8             | T                           |                            |                             |
|       | 33-53             | 7.5 yr 3.5/1                     | 52.4        | 73.8 23.3 2.9                             | LSa                           | 20.5           | 11.3 9.2                        | 1 1 59                                         | 7.7             | O                           |                            |                             |
|       | 53-81             | 7.5 yr 4.5/2                     | 74.4        | 72.8 23.8 3.4                             | LSa                           | 18.5           | 8.4 10.1                        | 1 2½ 64                                        | 7.8             | M                           |                            |                             |
| 3     | 0-2 <sup>8</sup>  |                                  | 11.2        |                                           |                               | 79.3           | 71.6 7.7                        | 7½ 9½ 148                                      | 6.4             | O                           |                            |                             |
|       | 2-10              | 7.5 yr 4/2                       | 15.9        | 71.8 23.8 3.4                             | SaL                           | 20.1           | 11.0 9.1                        | 10 5 124                                       | 6.7             | O                           |                            |                             |
|       | 10-28             | 7.5 yr 4.5/2                     | 39.4        | 62.1 33.1 4.8                             | SaL                           | 22.0           | 8.1 13.9                        | 1 2½ 108                                       | 6.6             | O                           |                            |                             |
|       | 28-81             | 7.5 yr 4.5/1.5                   | 67.7        | 88.5 8.2 3.3                              | Sa                            | 11.2           | 6.5 4.7                         | 1½ 2½ 60                                       | 7.5             | L                           |                            |                             |
| 4     | 8 ) 0             | 7.5 yr 3.5/1                     | 38.6        | 83.2 13.8 3.0                             | LSa                           | 12.0           | 7.2 4.8                         | 1 5 138                                        | 6.3             | O                           |                            |                             |
|       | 30 ) to           | 7.5 yr 4/2                       | 47.3        | 88.5 8.5 3.0                              | Sa                            | 7.9            | 5.0 2.9                         | 0 12 78                                        | 6.3             | O                           |                            |                             |
|       | 69 ) 90           | 10 yr 4.5/2.5                    | 56.7        | 88.4 7.7 3.9                              | Sa                            | 7.2            | 4.1 3.1                         | 0 12 60                                        | 6.4             | O                           |                            |                             |
| 5     | 0-10              | 10 yr 3/1.5                      | 1.3         | 69.8 25.3 4.9                             | SaL                           | 22.0           | 13.4 8.6                        | 9½ 5 162                                       | 6.9             | O                           |                            |                             |
|       | 10-25             | 10 yr 4/1.5                      | 0.8         | 67.7 25.4 6.9                             | SaL                           | 18.3           | 8.6 9.7                         | 2½ 2½ 96                                       | 7.5             | O                           |                            |                             |
|       | 25-86             | 10 yr 5/2                        | 60.4        | 87.0 7.2 5.8                              | LSa                           | 7.1            | 3.5 3.6                         | 1 2½ 66                                        | 7.8             | O                           |                            |                             |
| 6     | 0-5 <sup>8</sup>  |                                  | 15.7        |                                           |                               | 33.8           | 12.0 21.8                       | 3½ 11 200                                      | 7.4             | T                           |                            |                             |
|       | 5-18              | 5 yr 3.5/1.5                     | 48.5        | 75.7 21.2 3.1                             | LSa                           | 34.2           | 8.3 25.9                        | 3½ 3½ 102                                      | 6.4             | O                           |                            |                             |
|       | 18-74             | 5 yr 4.5/2                       | 75.1        | 88.6 9.2 2.2                              | Sa                            | 17.3           | 4.3 13.0                        | 1 3½ 35                                        | 6.7             | T                           |                            |                             |
|       | 74-90             | 5 yr 7.5/2                       | 28.2        | 66.0 29.3 4.7                             | SaL                           | 17.5           | 2.3 15.2                        | 1 ½ 25                                         | 8.0             | M                           |                            |                             |
| 7     | 0-5               | 5 yr 2/2                         | 39.5        | 70.2 25.3 4.5                             | SaL                           | 30.4           | 22.6 7.8                        | 1 9½ 216                                       | 6.4             | O                           |                            |                             |
|       | 5-25              | 5 yr 3/2                         | 71.8        | 86.8 11.1 2.1                             | Sa                            | 28.4           | 9.0 19.4                        | ½ 7½ 120                                       | 6.0             | O                           |                            |                             |
|       | 25-58             | 5 yr 3/1.5                       | 84.4        | 90.9 6.3 2.8                              | Sa                            | 24.1           | 6.0 18.1                        | 0 2½ 58                                        | 6.7             | O                           |                            |                             |
|       | 58-76             | 5 yr 5/2                         | 83.8        | 95.9 1.3 2.8                              | Sa                            | 8.3            | 3.0 5.3                         | 1 1 38                                         | 7.8             | M                           |                            |                             |
| 8     | 0-10              | 5 yr 3/2                         | 21.5        | 83.5 14.4 2.1                             | LSa                           | 16.7           | 9.2 7.5                         | 1 8½ 218                                       | 7.2             | L                           |                            |                             |
|       | 10-41             | 5 yr 3/2.5                       | 60.5        | 87.3 9.9 2.8                              | Sa                            | 10.8           | 5.3 5.5                         | 3½ 3½ 165                                      | 7.5             | O                           |                            |                             |
|       | 41-114            | 5 yr 3.5/2.5                     | 41.7        | 88.6 8.1 3.3                              | Sa                            | 12.2           | 5.1 7.1                         | 2½ 2½ 66                                       | 7.6             | O                           |                            |                             |
| 9     | 0-10 <sup>8</sup> | 5 yr 3.5/1.5                     | 0.0         |                                           |                               |                |                                 |                                                |                 |                             |                            |                             |
|       | 10-30             | 5 yr 4.5/1.5                     | 2.8         | 73.0 23.6 3.4                             | SaL                           | 25.8           | 15.1 10.7                       | 20½ 3½ 137                                     | 6.9             | O                           |                            |                             |
|       | 30-107            | 7.5 yr 5.5/2                     | 0.8         | 57.6 35.7 6.7                             | SaL                           | 21.2           | 5.7 15.5                        | 2 ½ 37                                         | 8.0             | T                           |                            |                             |



## APPENDIX 9. Cont'd.

| Stand               | Horizon (cm)     | Munsell <sup>1,2</sup> colour | Gravel % | Texture, % <sup>2</sup><br>Sand Silt Clay | Text. <sup>2,3</sup> class | Moisture FC | Char., % <sup>2,4</sup><br>PWP AW | Avail. Nutrients, ppm. <sup>2,5</sup><br>N P K | pH <sup>2</sup> | Free <sup>2,6</sup> Lime | Inorg. <sup>2,7</sup> % | Organic <sup>2,7</sup> % |
|---------------------|------------------|-------------------------------|----------|-------------------------------------------|----------------------------|-------------|-----------------------------------|------------------------------------------------|-----------------|--------------------------|-------------------------|--------------------------|
| 10                  | 0-8 <sup>8</sup> | 7.5 yr 3.5/1                  | 0.0      |                                           |                            |             |                                   |                                                |                 |                          |                         |                          |
|                     | 8-23             | 7.5 yr 4/1                    | 2.5      | 63.2 31.9 4.9                             | SaL                        | 25.9        | 10.8 15.1                         | 24½ 1 91                                       | 7.8             | L                        |                         |                          |
|                     | 23-58            | 7.5 yr 5/1.5                  | 1.2      | 49.6 41.8 8.6                             | SaL                        | 27.1        | 7.0 20.1                          | 4 1 43                                         | 8.1             | L                        |                         |                          |
| 11                  | 0-5              | 7.5 yr 3.5/1                  | 0.0      | 66.3 30.6 3.1                             | SaL                        | 31.6        | 17.5 14.1                         | ½ 6 218                                        | 6.2             | O                        |                         |                          |
|                     | 5-23             | 7.5 yr 4.5/2                  | 40.0     | 68.9 27.1 4.0                             | SaL                        | 21.1        | 7.7 13.4                          | 1 3½ 130                                       | 6.0             | O                        |                         |                          |
|                     | 23-64            | 7.5 yr 5/2                    | 74.3     | 68.9 27.1 4.0                             | SaL                        | 21.1        | 7.7 13.4                          | 1 3½ 130                                       | 6.0             | O                        |                         |                          |
|                     | 64-90            | 10 yr 6/3.5                   | 93.4     | 54.8 28.1 17.1                            | SaL                        | 24.6        | 7.9 16.7                          | 1½ 2½ 73                                       | 7.2             | O                        |                         |                          |
| 12                  | 0-13             | 10 yr 3.5/1.5                 | 3.1      | 59.8 34.1 6.1                             | SaL                        | 22.7        | 12.0 10.7                         | 1½ 2½ 262                                      | 6.2             | O                        |                         |                          |
|                     | 13-30            | 10 yr 4.5/1.5                 | 6.6      | 36.2 30.3 33.5                            | CL                         | 23.2        | 12.0 11.2                         | 1 1 300                                        | 5.9             | O                        |                         |                          |
|                     | 30-60            | 10 yr 5/2.5                   | 3.1      | 31.6 40.3 28.1                            | CL                         | 22.9        | 9.0 13.9                          | 1½ 2½ 145                                      | 6.0             | O                        |                         |                          |
|                     | 60-86            | 10 yr 5.5/2.5                 | 28.7     | 29.8 45.7 24.5                            | L                          | 24.6        | 7.7 16.9                          | 2½ ½ 148                                       | 7.6             | M                        |                         |                          |
| 13<br>5<br>to<br>30 | 0-5              | 7.5 yr 3.5/1.5                | 5.7      | 66.2 26.6 7.2                             | SaL                        | 33.7        | 21.6 12.1                         | 2 7½ 153                                       | 7.2             | O                        |                         |                          |
|                     | at 15            | 7.5 yr 5/2                    | 4.2      | 78.7 16.8 4.5                             | LSa                        | 11.4        | 4.6 6.8                           | 2½ 2½ 96                                       | 7.7             | O                        |                         |                          |
|                     | at 25            | 7.5 yr 5/2                    | 13.1     | 78.3 17.2 4.5                             | LSa                        | 11.9        | 4.2 7.7                           | 1 2½ 94                                        | 7.7             | O                        |                         |                          |
|                     | 30-51            | 7.5 yr 5.5/2                  | 42.1     | 89.4 6.6 4.0                              | Sa                         | 6.6         | 2.9 3.7                           | 1 1 81                                         | 8.0             | T                        |                         |                          |
|                     | 51-90            | 7.5 yr 5.5/2                  | 31.5     | 74.3 21.2 4.5                             | LSa                        | 14.0        | 4.6 9.4                           | 2½ 1 51                                        | 8.0             | T                        |                         |                          |
| 14                  | 0-5              | 7.5 yr 3/1                    | 29.4     | 81.1 12.1 6.8                             | LSa                        | 55.6        | 42.3 11.3                         | 3½ 8½ 300+                                     | 6.5             | O                        |                         |                          |
|                     | 5-13             | 7.5 yr 3/1                    | 18.6     | 75.4 21.2 3.1                             | LSa                        | 24.6        | 17.6 7.0                          | 4½ 3½ 204                                      | 6.1             | O                        |                         |                          |
|                     | 13-66            | 7.5 yr 4/1                    | 55.5     | 89.4 7.1 3.5                              | Sa                         | 11.2        | 6.7 4.5                           | 1½ 2½ 78                                       | 6.6             | O                        |                         |                          |
|                     | 66-90            | 7.5 yr 4.5/1                  | 11.4     | 60.4 28.2 11.4                            | SaL                        | 20.6        | 10.3 10.3                         | 1 1 58                                         | 7.3             | O                        |                         |                          |
| 15                  | 0-15             | 7.5 yr 4/1                    | 3.6      | 55.0 36.1 8.9                             | SaL                        | 28.5        | 14.0 14.5                         | ½ 2 118                                        | 6.2             | O                        |                         |                          |
|                     | 15-36            | 7.5 yr 4/1                    | 0.8      | 55.4 34.8 9.8                             | SaL                        | 26.6        | 12.9 13.7                         | 0 1 80                                         | 6.4             | O                        |                         |                          |
|                     | 36-90            | 7.5 yr 4.5/1.5                | 73.1     | 63.2 20.0 16.8                            | SaL                        | 12.4        | 6.3 6.1                           | 1½ 2 64                                        | 7.6             | T                        |                         |                          |
| 16                  | 0-30             | 10 yr 3.5/1                   | 19.8     | 63.5 30.0 6.5                             | SaL                        | 27.6        | 19.5 8.1                          | ½ 6 300+                                       | 6.1             | T                        |                         |                          |
|                     | 30-61            | 10 yr 4.5/2                   | 27.9     | 48.9 28.5 22.6                            | SaCL                       | 32.8        | 11.7 21.1                         | 0 2½ 268                                       | 6.0             | O                        |                         |                          |
|                     | 60-90            | 10 yr 4.5/2                   | 19.4     | 40.9 24.6 34.5                            | CL                         | 24.8        | 13.8 11.0                         | 1 1 158                                        | 6.7             | O                        |                         |                          |
| 17                  | 0-30             | 10 yr 3.5/1.5                 | 0.3      | 62.3 31.0 6.7                             | SaL                        | 17.3        | 9.3 8.0                           | 1 1 216                                        | 7.2             | O                        |                         |                          |
|                     | 30-60            | 10 yr 3.5/2                   | 0.1      | 58.6 33.2 8.2                             | SaL                        | 16.3        | 8.0 8.3                           | ½ 2 200                                        | 7.3             | O                        |                         |                          |
|                     | 60-90            | 10 yr 5/2                     | 0.0      | 48.5 32.1 19.4                            | L                          | ns          | 8.1 9.4                           | 1 ½ 83                                         | 7.9             | H                        |                         |                          |
| 18                  | 0-8              | 5 yr 2/1.5                    | 13.2     | 63.8 30.6 5.6                             | SaL                        | 38.9        | 30.9 8.0                          | 2 7½ 204                                       | 6.2             | O                        |                         |                          |
|                     | 8-30             | 5 yr 3.5/1.5                  | 55.8     | 78.4 18.1 3.5                             | LSa                        | 18.4        | 13.9 5.5                          | ½ 5½ 150                                       | 5.8             | O                        |                         |                          |
|                     | 30-76            | 5 yr 4.5/1.5                  | 69.2     | 90.4 5.9 3.7                              | Sa                         | 9.3         | 5.2 4.1                           | 0 4 57                                         | 6.8             | T                        |                         |                          |
|                     | 76-90            | 5 yr 4.5/1.5                  | 61.2     | 92.2 4.0 3.8                              | Sa                         | 7.7         | 4.9 2.8                           | 0 3 38                                         | 7.2             | T                        |                         |                          |





| Stand                          | Horizon<br>(cm)    | Munsell <sup>1,2</sup><br>colour | Gravel<br>% | Texture,<br>Sand | % <sup>2</sup><br>Silt | Clay | Text. <sup>2,3</sup><br>class | Moisture<br>FC | Char.,<br>PWP | % <sup>2,4</sup><br>AW | Avail. Nutrients, ppm. <sup>2,5</sup><br>N | P   | K    | pH <sup>2</sup> | Free <sup>2,6</sup><br>Lime | Inorg. <sup>2,7</sup><br>% | Organic <sup>2,7</sup><br>% |
|--------------------------------|--------------------|----------------------------------|-------------|------------------|------------------------|------|-------------------------------|----------------|---------------|------------------------|--------------------------------------------|-----|------|-----------------|-----------------------------|----------------------------|-----------------------------|
| 19                             | 0-5                | 7.5 yr 3/1                       | 14.5        | 59.2             | 35.0                   | 5.8  | SaL                           | 42.9           | 31.8          | 11.1                   | 2                                          | 13  | 300+ | 6.2             | O                           |                            |                             |
|                                | 5-30               | 7.5 yr 4.5/2                     | 66.9        | 79.5             | 16.4                   | 4.1  | LSa                           | 16.2           | 8.9           | 7.3                    | ½                                          | 3   | 93   | 6.5             | T                           |                            |                             |
|                                | 30-90              | 7.5 yr 5/2                       | 66.2        | 85.2             | 10.5                   | 4.3  | LSa                           | 11.4           | 5.4           | 6.0                    | ½                                          | 2   | 47   | 7.4             | T                           |                            |                             |
| 20                             | 0-8                | 7.5 yr 3/1.5                     | 22.0        | 73.0             | 20.6                   | 6.4  | SaL                           | 56.8           | 48.4          | 8.4                    | 2½                                         | 11  | 294  | 6.0             | O                           |                            |                             |
|                                | 8-25               | 7.5 yr 3/1                       | 48.9        | 72.2             | 24.4                   | 3.4  | SaL                           | 29.9           | 24.1          | 5.8                    | 1½                                         | 6   | 294  | 6.1             | O                           |                            |                             |
|                                | 25-76              | 7.5 yr 4.5/1                     | 59.9        | 78.6             | 16.4                   | 5.0  | LSa                           | 21.4           | 11.4          | 10.0                   | 0                                          | 5   | 300  | 6.0             | O                           |                            |                             |
| 21                             | 0-8                | 10 yr 2/2                        | 9.9         | 48.2             | 47.0                   | 4.8  | SaL                           | 44.2           | 33.6          | 10.6                   | 14½                                        | 5   | 156  | 7.5             | O                           |                            |                             |
|                                | 8-30               | 10 yr 5/1.5                      | 71.3        | 85.2             | 9.5                    | 5.3  | LSa                           | 20.5           | 5.6           | 14.9                   | 2½                                         | 1   | 150  | 7.8             | H                           |                            |                             |
|                                | 30-76              | 7.5 yr 4/1                       | 67.8        | 85.5             | 7.9                    | 6.6  | LSa                           | 24.6           | 2.4           | 22.2                   | 1                                          | 1   | 39   | 8.1             | H                           |                            |                             |
| 22<br>at 28(band) <sup>6</sup> | 0-4 <sup>8</sup>   | 5 yr 2.5/2                       |             |                  |                        |      |                               |                |               |                        |                                            |     |      |                 |                             |                            |                             |
|                                | 4-20               | 7.5 yr 5/1                       | 1.7         | 50.2             | 43.9                   | 5.9  | SaL                           | 39.0           | 26.4          | 12.6                   | 6                                          | 5   | 89   | 7.8             | L                           |                            |                             |
|                                | 20-36              | 7.5 yr 5/1                       | 1.8         | 55.6             | 37.5                   | 6.9  | SaL                           | 19.2           | 11.2          | 8.0                    | 2½                                         | 1   | 29   | 8.3             | H                           |                            |                             |
|                                |                    | 7.5 yr 4.5/2                     | 1.9         |                  |                        |      |                               | 24.4           | 14.9          | 9.5                    | 1                                          | 2½  | 73   | 8.1             | M                           |                            |                             |
|                                | 36-41              | 7.5 yr 5/1                       | 6.7         | 72.8             | 20.0                   | 7.2  | SaL                           | 21.3           | 11.9          | 9.4                    | 1½                                         | 1   | 20   | 8.3             | H                           |                            |                             |
|                                | 41-46 <sup>8</sup> | 5 yr 4/1                         | 2.9         | 46.6             | 42.5                   | 10.9 | L                             |                |               |                        | 1                                          | 0   | 42   | 8.2             | H                           |                            |                             |
|                                | 46-53              | 5 yr 6/3                         | 4.2         | 51.3             | 34.8                   | 13.9 | L                             | 34.8           | 13.6          | 21.2                   | ½                                          | 0   | 79   | 8.3             | H                           |                            |                             |
|                                | 53-90              | 10 yr 6/2                        | 16.4        | 46.2             | 38.0                   | 15.8 | L                             | 15.3           | 9.5           | 5.8                    | 0                                          | 0   | 72   | 8.3             | H                           |                            |                             |
|                                | 0-10               | 7.5 yr 2/1                       | 50.5        | 68.4             | 26.4                   | 5.2  | SaL                           | 46.7           | 33.6          | 13.1                   | 2                                          | 7½  | 144  | 6.7             | O                           |                            |                             |
|                                | 10-46 <sup>8</sup> | 7.5 yr 4/1                       | 88.0        | 90.5             | 5.0                    | 4.5  | Sa                            | 6.2            | 1.9           | 4.3                    |                                            |     |      |                 |                             |                            |                             |
|                                | 46-90              | 7.5 yr 4.5/1                     | 79.5        | 88.6             | 6.4                    | 5.0  | Sa                            | 5.2            | 2.4           | 2.8                    | 1½                                         | 1   | 29   | 7.8             | M                           |                            |                             |
| 24                             | 0-10 <sup>8</sup>  |                                  | 83.4        |                  |                        |      |                               | 95.5           | 87.0          | 8.5                    | 2½                                         | 15½ | 272  | 7.2             | O                           |                            |                             |
|                                | 10-76              | 7.5 yr 3/1                       | 78.1        | 65.0             | 29.6                   | 5.4  | SaL                           | 55.5           | 43.0          | 12.5                   | 2                                          | 3½  | 98   | 7.5             | L                           |                            |                             |
|                                | 76-90              | 10 yr 5/1.5                      | 78.1        | 71.3             | 22.2                   | 6.5  | SaL                           | 17.5           | 7.1           | 10.4                   | 2½                                         | 2   | 78   | 7.8             | H                           |                            |                             |
| 25                             | 0-20               | 10 yr 4/1                        | 4.4         | 48.2             | 46.2                   | 5.4  | SaL                           | 43.2           | 27.5          | 15.7                   | 9½                                         | 3   | 106  | 7.4             | M                           |                            |                             |
|                                | 20-33              | 10 yr 5/2                        | 0.2         | 48.4             | 42.4                   | 9.2  | SaL                           | 23.1           | 6.2           | 16.9                   | 2½                                         | ½   | 41   | 8.0             | H                           |                            |                             |
|                                | 33-38 <sup>8</sup> | 10 yr 5/2                        | 0.2         |                  |                        |      |                               |                |               |                        |                                            |     |      |                 |                             |                            |                             |
|                                | 38-56              | 10 yr 5/2                        | 0.2         | 48.4             | 42.4                   | 9.2  | SaL                           | 23.1           | 6.2           | 16.9                   | 2½                                         | ½   | 41   | 8.0             | H                           |                            |                             |
|                                | 46-69 <sup>8</sup> | 10 yr 4/1                        | 0.2         |                  |                        |      |                               |                |               |                        |                                            |     |      |                 |                             |                            |                             |
|                                | 69-90              | 10 yr 6/4                        | 13.6        | 40.5             | 45.1                   | 14.4 | L                             | 34.0           | 8.9           | 25.1                   | 1                                          | 1   | 60   | 8.0             | T                           |                            |                             |
| 26                             | 0-18               | 7.5 yr 2/2                       | 49.0        | 43.0             | 50.1                   | 6.9  | SaL                           | 104.5          | 92.0          | 12.5                   | 1½                                         | 9½  | 174  | 7.4             | O                           |                            |                             |
|                                | 18-46              | 7.5 yr 3/1                       | 69.6        | 51.4             | 44.0                   | 4.6  | SaL                           | 50.5           | 30.4          | 20.1                   | 6½                                         | 1   | 119  | 7.9             | M                           |                            |                             |
|                                | 46-66              | 7.5 yr 3.5/3                     | 67.2        | 53.2             | 41.4                   | 5.4  | SaL                           | 41.2           | 18.6          | 22.6                   | 4½                                         | 1   | 190  | 8.0             | L                           |                            |                             |
|                                | 66-84              | 10 yr 4.5/3.5                    | 58.7        | 39.4             | 56.2                   | 4.4  | SiL                           | 51.0           | 18.3          | 32.7                   | 2½                                         | 0   | 147  | 8.1             | L                           |                            |                             |



## APPENDIX 9. Cont'd.

| Stand                  | Horizon (cm)       | Munsell <sup>1,2</sup> colour | Gravel % | Texture, Sand | Silt | % <sup>2</sup> Clay | Text. <sup>2,3</sup> class | Moisture FC | Char., PWP | % <sup>2,4</sup> AW | Avail. Nutrients, ppm. <sup>2,5</sup> N | P  | K    | pH <sup>2</sup> | Free <sup>2,6</sup> Lime | Inorg. <sup>2,7</sup> % | Organic <sup>2,7</sup> % |
|------------------------|--------------------|-------------------------------|----------|---------------|------|---------------------|----------------------------|-------------|------------|---------------------|-----------------------------------------|----|------|-----------------|--------------------------|-------------------------|--------------------------|
| 27                     | 0-2                |                               | 53.0     | 55.3          | 41.6 | 3.1                 | SaL                        | 36.6        | 24.9       | 11.7                | 0                                       | 2½ | 227  | 7.4             | O                        |                         |                          |
|                        | 2-18               | 10 yr 3.5/1                   | 57.7     | 88.6          | 7.9  | 3.5                 | Sa                         | 7.0         | 2.8        | 4.2                 | 2½                                      | 0  | 25   | 8.0             | H                        |                         |                          |
|                        | 18-79              | 10 yr 5/2                     | 66.4     | 89.6          | 6.7  | 3.7                 | Sa                         | 5.8         | 2.5        | 3.3                 | 2½                                      | 0  | 20   | 8.1             | H                        |                         |                          |
| 27 low spot            | 0-2                | 7.5 yr 3/1                    | 6.4      | 46.4          | 47.3 | 6.3                 | SaL                        | 52.9        | 27.7       | 25.2                | 1                                       | 5½ | 246  | 7.6             | M                        |                         |                          |
|                        | 2-25               | 7.5 yr 4/1                    | 0.6      | 56.4          | 37.3 | 6.3                 | SaL                        | 40.5        | 16.3       | 24.2                | ½                                       | 1  | 70   | 7.9             | M                        |                         |                          |
|                        | 25-38              | 7.5 yr 5/4                    | 1.6      | 59.7          | 33.1 | 7.2                 | SaL                        | 23.4        | 9.5        | 13.9                | 2                                       | 0  | 73   | 8.0             | T                        |                         |                          |
|                        | 38-69              | 10 yr 5/1.5                   | 0.0      | 48.4          | 41.9 | 9.7                 | SaL                        | 22.8        | 6.7        | 16.1                | 1½                                      | ½  | 30   | 8.2             | H                        |                         |                          |
| 28                     | 0-10               | 10 yr 3/1.5                   | 36.4     | 57.3          | 39.8 | 2.9                 | SaL                        | 35.2        | 21.4       | 13.8                | 1                                       | 2½ | 90   | 7.4             | T                        |                         |                          |
|                        | 10-41              | 10 yr 6/1.5                   | 77.9     | 83.2          | 10.8 | 6.0                 | LSa                        | 11.4        | 5.6        | 5.8                 | 2                                       | 1  | 23   | 8.2             | H                        |                         |                          |
|                        | 41-60              | 10 yr 6.5/1.5                 | 68.0     | 84.7          | 7.6  | 7.7                 | LSa                        | 6.2         | 2.2        | 4.0                 | 1½                                      | 0  | 18   | 8.1             | H                        |                         |                          |
| 29                     | 0-5                | 7.5 yr 2/2                    | 10.2     | 48.4          | 46.2 | 5.4                 | SaL                        | 41.1        | 27.2       | 13.9                | 3                                       | 7½ | 260  | 6.7             | O                        |                         |                          |
|                        | 5-10               | 7.5 yr 3/2                    | 71.5     | 60.9          | 29.5 | 9.6                 | SaL                        | 28.7        | 17.3       | 11.4                | 0                                       | 5  | 165  | 6.8             | O                        |                         |                          |
|                        | 10-30 <sup>9</sup> |                               |          |               |      |                     |                            |             |            |                     |                                         |    |      |                 |                          |                         |                          |
| 30                     | 0-8                | 10 yr 2/3                     | 1.6      | 56.2          | 40.0 | 3.8                 | SaL                        | 44.9        | 36.3       | 8.6                 | 12½                                     | 3½ | 300+ | 6.9             | O                        |                         |                          |
|                        | 8-30               | 7.5 yr 3/1                    | 9.0      | 53.4          | 32.9 | 13.7                | SaL                        | 33.2        | 20.5       | 12.7                | 0                                       | 1  | 220  | 7.2             | T                        |                         |                          |
|                        | 30-76              | 5 yr 5/1.5                    | 5.7      | 56.7          | 28.1 | 15.2                | SaL                        | 46.6        | 24.0       | 22.6                | 1½                                      | ½  | 55   | 8.3             | H                        |                         |                          |
|                        | 76-102             | 5 yr 4.5/1                    | 1.8      | 34.1          | 36.3 | 29.6                | CL                         | 25.2        | 8.4        | 16.8                | 0                                       | ½  | 47   | 8.7             | H                        |                         |                          |
| 31 <sup>0 to 102</sup> | 0-13               | 10 yr 3/2                     | 11.5     | 66.5          | 30.3 | 3.2                 | SaL                        | 26.3        | 16.1       | 10.2                | 3                                       | 3½ | 126  | 7.4             | O                        |                         |                          |
|                        | at 30              | 10 yr 4/1                     | 68.4     | 78.8          | 17.6 | 3.6                 | LSa                        | 13.4        | 6.8        | 6.6                 | ½                                       | 6  | 134  | 8.0             | M                        |                         |                          |
|                        | at 90              | 10 yr 4.5/1                   | 63.6     | 84.6          | 11.5 | 3.9                 | LSa                        | 9.9         | 5.3        | 4.6                 | 0                                       | 6  | 192  | 8.0             | M                        |                         |                          |
| 32                     | 0-5                | 7.5 yr 3.5/1.5                | 20.5     | 51.1          | 39.2 | 9.7                 | SaL                        | 31.9        | 13.0       | 18.9                | 3½                                      | 3½ | 153  | 7.9             | M                        |                         |                          |
|                        | 5-8                | 7.5 yr 5/3                    | 13.9     | 54.2          | 36.2 | 9.6                 | SaL                        |             |            |                     | 1                                       | 1  | 69   | 8.1             | VH                       |                         |                          |
|                        | 8-30               | 7.5 yr 4/2                    | 72.1     | 67.7          | 26.9 | 5.4                 | SaL                        | 25.4        | 13.3       | 12.1                | 2½                                      | 2  | 125  | 8.0             | VH                       |                         |                          |
|                        | 30-60              | 7.5 yr 5/2                    | 61.0     | 77.3          | 18.3 | 4.4                 | LSa                        | 22.4        | 11.1       | 11.3                | ½                                       | 1  | 70   | 7.9             | H                        |                         |                          |
| 33                     | 0-5                | 5 yr 3.5/3                    | 0.7      | 41.9          | 46.3 | 11.6                | L                          | 59.1        | 40.1       | 19.0                | 0                                       | 5  | 239  | 7.5             | O                        |                         |                          |
|                        | 5-15               | 7.5 yr 5/3                    | 0.3      | 62.7          | 30.4 | 6.9                 | SaL                        | 31.3        | 14.8       | 16.5                | 0                                       | 1  | 156  | 7.4             | O                        |                         |                          |
|                        | 15-28              | 10 yr 5/2                     | 1.0      | 54.0          | 38.7 | 7.3                 | SaL                        | 24.0        | 9.1        | 14.9                | ½                                       | 1  | 60   | 7.9             | H                        |                         |                          |
|                        | 28-76              | 10 yr 6/1.5                   | 69.8     | 77.6          | 15.4 | 7.0                 | LSa                        | 16.0        | 7.5        | 8.5                 | ½                                       | 1  | 58   | 8.1             | VH                       |                         |                          |
| 34                     | 0-8                | 10 yr 4/1                     | 1.1      | 73.5          | 17.3 | 19.2                | SaL                        | 47.7        | 36.6       | 11.1                | ½                                       | 2½ | 234  | 7.1             | O                        |                         |                          |
|                        | 8-33               | 10 yr 6/2.5                   | 0.0      | 20.2          | 52.6 | 27.5                | CL                         | 29.0        | 11.1       | 17.9                | 0                                       | 1  | 62   | 7.9             | M                        |                         |                          |
|                        | 33-48              | 10 yr 6.5/2.5                 | 0.0      | 20.2          | 47.7 | 32.1                | CL                         | 32.2        | 13.5       | 18.7                | ½                                       | 0  | 57   | 8.2             | M                        |                         |                          |
|                        | 48-76              | 10 yr 7/2                     | 0.0      | 22.8          | 44.9 | 32.7                | CL                         | 33.9        | 14.3       | 19.6                | 0                                       | 1  | 58   | 8.3             | H                        |                         |                          |
| 35                     | 0-13               | 10 yr 5/1.5                   | 0.0      | 65.9          | 27.8 | 6.3                 | SaL                        | 15.5        | 5.3        | 10.2                | 0                                       | 1  | 44   | 8.0             | M                        |                         |                          |
|                        | 13-28              | 10 yr 5/1.5                   | 1.5      | 61.8          | 31.6 | 6.6                 | SaL                        | 19.3        | 6.0        | 13.3                | 1                                       | 1  | 29   | 8.1             | H                        |                         |                          |
|                        | 28-33 <sup>8</sup> |                               | 50.7     | 58.0          | 35.9 | 6.1                 | SaL                        | 25.8        | 12.1       | 13.7                | 0                                       | 1  | 42   | 8.0             | H                        |                         |                          |
|                        | 33-48              | 10 yr 5.5/1.5                 | 1.1      | 66.3          | 26.9 | 6.8                 | SaL                        | 17.3        | 6.8        | 10.5                | 1                                       | 0  | 26   | 8.1             | H                        |                         |                          |





## APPENDIX 9. Cont'd.

| Stand | Horizon<br>(cm)                 | Munsell <sup>1,2</sup><br>colour | Gravel<br>%                     | Texture, %<br>Sand Silt Clay |      |      | Text. <sup>2,3</sup><br>class | Moisture<br>FC | Char.,<br>PWP | % <sup>2,4</sup><br>AW | Avail. Nutrients, ppm. <sup>2,5</sup><br>N P K |    |      | pH <sup>2</sup> | Free<br>Lime | Inorg. <sup>2,7</sup><br>% | Organic <sup>2,7</sup><br>% |
|-------|---------------------------------|----------------------------------|---------------------------------|------------------------------|------|------|-------------------------------|----------------|---------------|------------------------|------------------------------------------------|----|------|-----------------|--------------|----------------------------|-----------------------------|
|       | 48-76                           | 10 yr 5.5/1                      | 34.2                            | 80.9                         | 11.8 | 7.3  | LSa                           | 8.0            | 3.2           | 4.8                    | 0                                              | 0  | 20   | 8.2             | H            |                            |                             |
| 36    | 0-25                            | 10 yr 4/1.5                      | 0.4                             | 44.5                         | 52.3 | 3.2  | SiL                           | 10.6           | 8.8           | 1.8                    | ½                                              | 0  | 41   | 8.0             | H            |                            |                             |
|       | 25-60                           | 10 yr 4.5/1.5                    | 0.0                             | 77.6                         | 19.4 | 3.0  | LSa                           | 5.9            | 3.5           | 2.4                    | ½                                              | 0  | 83   | 8.0             | H            |                            |                             |
|       | 60-86                           | 10 yr 4.5/1.5                    | 7.2                             | 74.9                         | 20.9 | 4.2  | LSa                           | 15.8           | 3.7           | 12.1                   | ½                                              | 0  | 128  | 8.0             | H            |                            |                             |
|       | 0 )at 8                         | 10 yr 5.5/1.5                    | 0.4                             | 15.6                         | 75.7 | 8.7  | SiL                           | 11.7           | 4.3           | 7.4                    | ½                                              | 0  | 30   | 8.1             | H            |                            |                             |
| 37    | to )at 30                       | 10 yr 5.5/1.5                    | 1.4                             | 16.9                         | 74.9 | 8.2  | SiL                           | 5.8            | 5.4           | 0.4                    | 1                                              | 1  | 20   | 8.1             | H            |                            |                             |
|       | 90 )at 69                       | 10 yr 5.5/1.5                    | 0.0                             | 13.3                         | 79.1 | 7.6  | Si                            | 5.3            | 4.4           | 1.4                    | 1                                              | 0  | 20   | 8.3             | H            |                            |                             |
| 38    | 0-5 <sup>a</sup>                |                                  | 0.0                             |                              |      |      |                               |                |               |                        |                                                |    |      |                 |              |                            |                             |
|       | 5-18                            | 10 yr 6/1                        | 37.2                            | 60.5                         | 35.0 | 4.5  | SaL                           | 35.1           | 12.6          | 22.5                   | 1½                                             | ½  | 99   | 8.0             | H            |                            |                             |
|       | 18-48                           | 10 yr 5/1                        | 45.0                            | 90.3                         | 4.0  | 5.7  | Sa                            | 5.3            | 1.9           | 3.4                    | 1                                              | ½  | 20   | 8.3             | H            |                            |                             |
|       | 48-60                           | 2.5 yr 7.5/2                     | 0.0                             | 7.2                          | 29.1 | 63.7 | HC                            | 36.8           | 19.6          | 17.2                   | 1½                                             | 1  | 53   | 8.3             | H            |                            |                             |
|       | 60-74                           | 10 yr 5/1                        | Gravel and boulders: no sample. |                              |      |      |                               |                |               |                        |                                                |    |      |                 |              |                            |                             |
|       | 74-86                           | 2.5 yr 7.5/2                     | 0.0                             | 7.2                          | 29.1 | 63.7 | HC                            | 36.8           | 19.6          | 17.2                   | 1½                                             | 1  | 53   | 8.3             | H            |                            |                             |
| 39    | 0-5                             | 10 yr 4/1.5                      | 1.4                             | 39.8                         | 56.2 | 4.0  | SiL                           | 27.7           | 11.5          | 16.2                   | ½                                              | 1  | 68   | 7.8             | H            |                            |                             |
|       | 5-30                            | 10 yr 4/1.5                      | 0.7                             | 42.7                         | 50.1 | 7.2  | SaL                           | 25.8           | 6.9           | 18.9                   | 1½                                             | 0  | 34   | 8.2             | H            |                            |                             |
|       | 30-90                           | 10 yr 4/1                        | 70.3                            | 92.1                         | 2.7  | 5.2  | Sa                            | 4.3            | 2.1           | 2.2                    | 1½                                             | 0  | 58   | 8.0             | H            |                            |                             |
| 40    | 0-10                            | 5 yr 4/1                         | 5.4                             | 25.0                         | 31.2 | 43.8 | C                             | 60.0           | 18.8          | 41.2                   | 1                                              | 3½ | 161  | 5.5             | O            |                            |                             |
|       | 10-46                           | 2.5 yr 7/2                       | 0.1                             | 0.8                          | 36.0 | 53.5 | HC                            | 43.1           | 12.8          | 30.3                   | 2                                              | 1  | 41   | 5.4             | O            |                            |                             |
|       | 46-84                           | 2.5 yr 6.5/2                     | 0.0                             | 8.9                          | 37.7 | 50.5 | C                             | 42.5           | 16.9          | 25.6                   | 3½                                             | 1  | 44   | 5.9             | O            |                            |                             |
|       | Bare spot<br>2-18 <sup>10</sup> |                                  | 0.0                             | 1.3                          | 37.0 | 54.0 | HC                            | 45.7           | 13.6          | 32.1                   | 40+                                            | 2½ | 141  | 4.6             | O            |                            |                             |
| 41    | 0-5 <sup>a</sup>                | 10 yr 5/1                        | 0.0                             |                              |      |      |                               |                |               |                        |                                                |    |      |                 |              |                            |                             |
|       | 5-25                            | 10 yr 6.5/1.5                    | 0.1                             | 50.0                         | 20.9 | 29.1 | SaCL                          | 43.8           | 21.2          | 22.6                   | 1                                              | 1  | 104  | 7.6             | O            |                            |                             |
|       | 25-46+                          | 10 yr 5/1.5                      | 2.5                             | 67.7                         | 12.3 | 20.0 | SaL                           | 37.1           | 22.6          | 14.5                   | 1                                              | 1  | 94   | 7.5             | O            |                            |                             |
| 42    | 0-8                             | 5 yr 4/1.5                       | 1.0                             | 49.3                         | 43.5 | 7.2  | SaL                           | 38.7           | 15.0          | 23.7                   | 1                                              | 3½ | 300+ | 7.8             | M            |                            |                             |
|       | 8-30                            | 5 yr 5/3                         | 0.8                             | 53.9                         | 34.7 | 11.4 | SaL                           | 32.6           | 13.3          | 19.3                   | ½                                              | 1  | 300+ | 8.1             | M            |                            |                             |
|       | 30-64                           | 5 yr 4/1                         | 0.1                             | 40.9                         | 36.0 | 23.1 | L                             | 33.0           | 17.3          | 15.7                   | ½                                              | ½  | 98   | 8.2             | H            |                            |                             |
|       | 64-74                           | 5 yr 5/1                         | 22.5                            | 35.6                         | 34.7 | 29.7 | CL                            | 31.9           | 15.5          | 16.4                   | ½                                              | ½  | 51   | 8.4             | H            |                            |                             |
|       | 74-90                           | 5 yr 5/1                         | 0.4                             | 28.5                         | 43.3 | 28.2 | CL                            | 33.1           | 10.8          | 22.3                   | ½                                              | ½  | 34   | 8.6             | H            |                            |                             |
| 43    | 0-2                             | 10 yr 6/2                        | 1.2                             | 61.2                         | 34.6 | 4.2  | SaL                           | 23.6           | 7.7           | 15.9                   | 1                                              | 2½ | 120  | 8.0             | H            |                            |                             |
|       | 2-51                            | 10 yr 6/2                        | 2.9                             | 89.1                         | 5.7  | 5.2  | Sa                            | 9.0            | 3.1           | 5.9                    | ½                                              | 2  | 23   | 8.4             | H            |                            |                             |
|       | 51-86                           | 10 yr 5.5/2                      | 8.5                             | 95.7                         | 0.4  | 3.9  | Sa                            | 2.4            | 0.7           | 1.7                    | 1                                              | 1  | 8    | 8.6             | M            |                            |                             |



| Stand          | Horizon             |     | Munsell <sup>1,2</sup> |         | Gravel<br>% | Texture, % <sup>2</sup> |      |      | Text. <sup>2,3</sup><br>class | Moisture<br>FC | Char.,<br>PWP | % <sup>2,4</sup> |     | Avail. Nutrients, ppm. <sup>2,5</sup> |     |     |      | pH <sup>2</sup> | Free <sup>2,6</sup> |   | Inorg. <sup>2,7</sup> |  | Organic <sup>2,7</sup> |  |
|----------------|---------------------|-----|------------------------|---------|-------------|-------------------------|------|------|-------------------------------|----------------|---------------|------------------|-----|---------------------------------------|-----|-----|------|-----------------|---------------------|---|-----------------------|--|------------------------|--|
|                | (cm)                |     | colour                 |         |             | Sand                    | Silt | Clay |                               |                |               | AW               | N   | P                                     | K   |     | Lime |                 | %                   | % |                       |  |                        |  |
| 44             | 0-5                 | 7.5 | yr                     | 3/1.5   | 2.2         | 43.0                    | 45.4 | 11.6 | L                             | 35.8           | 11.9          | 23.9             | ½   | 2½                                    | 102 | 7.8 | H    |                 |                     |   |                       |  |                        |  |
|                | 5-10                | 7.5 | yr                     | 3/1.5   | 0.2         | 42.3                    | 45.5 | 12.2 | L                             | 59.4           | 12.2          | 27.2             | ½   | 1                                     | 76  | 7.9 | H    |                 |                     |   |                       |  |                        |  |
|                | 10-20               | 10  | yr                     | 4/1.5   | 0.1         | 52.8                    | 38.4 | 8.8  | SaL                           | 20.5           | 5.9           | 14.6             | 1   | 0                                     | 42  | 8.1 | H    |                 |                     |   |                       |  |                        |  |
|                | 20-30               | 10  | yr                     | 4.5/1.5 | 14.2        | 88.1                    | 7.9  | 4.0  | Sa                            | 6.3            | 2.6           | 3.7              | ½   | 0                                     | 42  | 8.1 | H    |                 |                     |   |                       |  |                        |  |
|                | 30-84               | 10  | yr                     | 4/1.5   | 65.4        | 75.8                    | 15.0 | 9.2  | SaL                           | 9.0            | 3.5           | 5.5              | 1   | ½                                     | 44  | 8.2 | H    |                 |                     |   |                       |  |                        |  |
| 45             | 0-10                | 10  | yr                     | 5/1.5   | 1.9         | 51.6                    | 42.7 | 5.7  | SaL                           | 33.5           | 12.6          | 20.9             | 3½  | 2½                                    | 158 | 8.0 | H    |                 |                     |   |                       |  |                        |  |
|                | 10-36               | 10  | yr                     | 6/1.5   | 0.3         | 66.0                    | 29.6 | 4.4  | SaL                           | 25.1           | 10.5          | 14.6             | 0   | 1                                     | 41  | 8.3 | H    |                 |                     |   |                       |  |                        |  |
|                | 36-60               | 10  | yr                     | 6.5/2   | 27.5        | 73.3                    | 20.5 | 6.2  | SaL                           | 15.4           | 7.0           | 8.4              | 0   | 0                                     | 26  | 8.4 | H    |                 |                     |   |                       |  |                        |  |
|                | 60-76               | 10  | yr                     | 6.5/1.5 | 63.2        | 75.0                    | 19.6 | 5.4  | SaL                           | 17.0           | 6.9           | 10.1             | ½   | 0                                     | 34  | 8.3 | H    |                 |                     |   |                       |  |                        |  |
| 46<br>to<br>90 | 0-2                 | 10  | yr                     | 5.5/1.5 | 1.5         | 55.0                    | 35.3 | 9.7  | SaL                           | 39.9           | 16.6          | 23.3             | ½   | 5                                     | 115 | 6.2 | T    |                 |                     |   |                       |  |                        |  |
|                | at 15               | 10  | yr                     | 5.5/1.5 | 0.0         | 32.1                    | 51.4 | 16.5 | SiL                           | 37.9           | 12.6          | 25.3             | 0   | 3½                                    | 42  | 6.1 | O    |                 |                     |   |                       |  |                        |  |
|                | at 60               | 10  | yr                     | 5.5/1.5 | 0.3         | 11.5                    | 49.2 | 39.3 | SiCL                          | 31.8           | 13.0          | 18.8             | 0   | 3½                                    | 74  | 6.3 | O    |                 |                     |   |                       |  |                        |  |
| 47             | 0-13                | 10  | yr                     | 6/1.5   | 0.1         | 36.9                    | 51.3 | 11.8 | SiL                           | 25.7           | 6.5           | 19.2             | 0   | 0                                     | 58  | 8.0 | H    |                 |                     |   |                       |  |                        |  |
|                | 13-28               | 10  | yr                     | 5.5/1   | 0.3         | 40.9                    | 48.7 | 10.4 | L                             | 24.4           | 8.1           | 16.3             | ½   | 0                                     | 99  | 8.0 | H    |                 |                     |   |                       |  |                        |  |
|                | 28-33 <sup>8</sup>  |     |                        |         | 68.7        | 54.7                    | 30.3 | 15.0 | SaL                           | 24.8           | 9.3           | 15.5             | 0   | 1                                     | 91  | 8.1 | H    |                 |                     |   |                       |  |                        |  |
|                | 33-48               | 10  | yr                     | 5.5/2   | 6.1         | 49.6                    | 35.5 | 14.9 | L                             | 29.1           | 7.1           | 22.0             | 0   | 1                                     | 86  | 8.1 | H    |                 |                     |   |                       |  |                        |  |
|                | 48-66               | 10  | yr                     | 6/1.5   | 1.6         | 46.3                    | 44.3 | 9.4  | SaL                           | 19.4           | 4.6           | 14.8             | 0   | 0                                     | 66  | 7.8 | H    |                 |                     |   |                       |  |                        |  |
|                | 66-76               | 7.5 | yr                     | 6/2     | 7.2         | 42.8                    | 47.5 | 9.7  | SaL                           | 32.9           | 9.6           | 23.3             | 0   | 0                                     | 165 | 8.0 | H    |                 |                     |   |                       |  |                        |  |
|                | 76-90               | 7.5 | yr                     | 5/2     | 54.4        | 57.6                    | 33.3 | 9.1  | SaL                           | 23.9           | 8.7           | 15.2             | 0   | 1                                     | 74  | 7.9 | H    |                 |                     |   |                       |  |                        |  |
| 48             | 0-13                | 10  | yr                     | 4.5/1.5 | 0.3         | 40.0                    | 53.2 | 6.8  | SiL                           | 17.9           | 6.5           | 11.4             | 3   | 1                                     | 68  | 7.9 | H    |                 |                     |   |                       |  |                        |  |
|                | 13-25               | 7.5 | yr                     | 4.5/1.5 | 0.6         | 39.0                    | 53.5 | 7.5  | SiL                           | 25.1           | 9.9           | 15.2             | 3½  | 0                                     | 42  | 8.0 | H    |                 |                     |   |                       |  |                        |  |
|                | 25-76 <sup>11</sup> | 10  | yr                     | 6/2     | 0.0         | 39.2                    | 52.3 | 8.5  | SiL                           | 26.2           | 9.4           | 16.8             | 18  | 0                                     | 66  | 8.4 | H    |                 |                     |   |                       |  |                        |  |
|                | 76-90 <sup>12</sup> | 10  | yr                     | 6.5/2   | 51.8        | 64.3                    | 21.8 | 13.9 | SaL                           | 12.4           | 5.8           | 6.6              | 11½ | 1                                     | 62  | 8.7 | H    |                 |                     |   |                       |  |                        |  |
| 49             | 0-10                | 7.5 | yr                     | 4/1     | 0.3         | 60.9                    | 32.3 | 6.8  | SaL                           | 20.0           | 9.2           | 10.8             | 3   | 1                                     | 80  | 7.9 | H    |                 |                     |   |                       |  |                        |  |
|                | 10-30               | 10  | yr                     | 5.5/3   | 0.3         | 90.9                    | 1.2  | 6.9  | Sa                            | 4.9            | 2.0           | 2.9              | ½   | 1                                     | 17  | 8.2 | H    |                 |                     |   |                       |  |                        |  |
|                | 30-102              | 10  | yr                     | 5.5/2.5 | 0.4         | 92.6                    | 0.9  | 6.5  | Sa                            | 3.2            | 0.9           | 2.3              | ½   | 1                                     | 7   | 8.4 | M    |                 |                     |   |                       |  |                        |  |
| 50             | 0-5                 | 10  | yr                     | 3.5/1   | 0.8         | 51.2                    | 36.6 | 12.2 | SaL                           | 49.9           | 38.4          | 11.5             | 0   | 7½                                    | 138 | 6.0 | O    |                 |                     |   |                       |  |                        |  |
|                | 5-15                | 10  | yr                     | 5/1.5   | 0.0         | 38.7                    | 53.3 | 8.0  | SiL                           | 31.7           | 9.7           | 22.0             | 0   | 3½                                    | 34  | 7.7 | T    |                 |                     |   |                       |  |                        |  |
|                | 15-20               | 10  | yr                     | 5.5/3   | 0.4         | 17.8                    | 55.3 | 26.9 | SiL                           | 28.9           | 10.7          | 18.2             | 0   | 2½                                    | 52  | 7.9 | O    |                 |                     |   |                       |  |                        |  |
|                | 20-30               | 10  | yr                     | 6/2     | 0.1         | 4.8                     | 72.5 | 22.7 | SiL                           | 30.8           | 7.7           | 23.1             | 0   | 2                                     | 27  | 8.2 | M    |                 |                     |   |                       |  |                        |  |
|                | 30-36               | 7.5 | yr                     | 6.5/4   | 2.2         | 25.0                    | 46.8 | 28.2 | CL                            | 23.4           | 7.3           | 16.1             | 0   | 3½                                    | 37  | 8.2 | M    |                 |                     |   |                       |  |                        |  |
|                | 36-69               | 7.5 | yr                     | 5.5/2   | 70.5        | 54.9                    | 25.6 | 19.5 | SaL                           | 18.7           | 9.5           | 9.2              | 0   | 5                                     | 65  | 8.1 | M    |                 |                     |   |                       |  |                        |  |
| 51             | 0-4 <sup>8</sup>    |     |                        |         | 1.9         | 60.9                    | 33.1 | 6.0  | SaL                           | 33.7           | 25.2          | 8.5              | 0   | 7½                                    | 164 | 7.4 | L    |                 |                     |   |                       |  |                        |  |
|                | 4-13                | 10  | yr                     | 4/1     | 0.3         | 64.9                    | 29.4 | 5.7  | SaL                           | 23.4           | 14.8          | 8.6              | 0   | 5                                     | 65  | 7.7 | M    |                 |                     |   |                       |  |                        |  |



| Stand | Horizon (cm)       | Munsell <sup>1,2</sup> colour | Gravel %                                     | Texture, % <sup>2</sup><br>Sand Silt Clay | Text. <sup>2,3</sup> class | Moisture Char., % <sup>2,4</sup><br>FC PWP AW | Avail. Nutrients, ppm. <sup>2,5</sup><br>N P K | pH <sup>2</sup> | Free <sup>2,6</sup> Lime | Inorg. <sup>2,7</sup> % | Organic <sup>2,7</sup> % |
|-------|--------------------|-------------------------------|----------------------------------------------|-------------------------------------------|----------------------------|-----------------------------------------------|------------------------------------------------|-----------------|--------------------------|-------------------------|--------------------------|
|       | 13-23              | 10 yr 6/2                     | 2.9                                          | 62.4 31.6 6.0                             | SaL                        | 12.1 4.5 7.6                                  | 0 1 31                                         | 7.9             | H                        |                         |                          |
|       | 23-30              |                               | Gravel and Boulders: no sample.              |                                           |                            |                                               |                                                |                 |                          |                         |                          |
|       | 30-76              | 10 yr 5/1.5                   | 39.7                                         | 86.7 7.4 5.9                              | LSa                        | 3.6 1.6 2.0                                   | 0 1 24                                         | 8.2             | H                        |                         |                          |
|       | 76-90 <sup>8</sup> |                               | 73.4                                         | 87.5 5.5 7.0                              | LSa                        | 3.0 1.3 1.7                                   | 0 1 18                                         | 8.4             | H                        |                         |                          |
| 52    | 0-10               | 5 yr 3.5/2                    | 0.0                                          | 48.6 47.7 3.7                             | SaL                        | 23.7 10.8 12.9                                | ½ 0 105                                        | 8.0             | H                        | 4.3                     | 4.3                      |
|       | 10-30              | 5 yr 5/2                      | 0.0                                          | 66.1 27.6 6.3                             | SaL                        | 23.8 12.4 11.4                                | ½ 0 57                                         | 8.4             | H                        | 2.1                     | 1.6                      |
|       | 30-53              | 7.5 yr 6/3                    | 0.0                                          | 85.4 8.7 5.9                              | LSa                        | 9.8 2.8 7.0                                   | ½ 0 39                                         | 8.7             | H                        |                         |                          |
|       | 53-56              |                               | No sample taken, coarse gravel and boulders. |                                           |                            |                                               |                                                |                 |                          |                         |                          |
|       | 56-90              | 10 yr 5.5/2.5                 | 1.0                                          | 95.5 1.6 2.9                              | Sa                         | 3.0 0.8 2.2                                   | ½ 0 18                                         | 9.1             | H                        |                         |                          |
| 53    | 0-10               | 7.5 yr 3.5/2                  | 0.0                                          | 50.7 44.6 4.7                             | SaL                        | 27.5 11.8 15.7                                | ½ 0 76½                                        | 8.1             | H                        | 3.8                     | 4.2                      |
|       | 10-28              | 7.5 yr 5/2.5                  | 0.1                                          | 73.7 19.0 7.3                             | SaL                        | 12.7 5.5 7.2                                  | ½ 0 78                                         | 8.4             | H                        | 0.8                     | 1.3                      |
|       | 28-90              | 10 yr 6/2.5                   | 0.0                                          | 94.5 1.6 3.9                              | Sa                         | 3.7 1.0 2.7                                   | ½ 1 16                                         | 8.6             | H                        |                         |                          |
| 54    | 0-5                | 7.5 yr 3.5/2                  | 0.1                                          | 61.7 34.8 3.5                             | SaL                        | 27.7 12.2 15.5                                | ½ 2½ 109                                       | 7.9             | H                        | 1.7                     | 4.7                      |
|       | 5-15               | 10 yr 6/2.5                   | 0.1                                          | 76.3 18.8 4.9                             | LSa                        | 11.4 3.4 8.0                                  | 0 2 57                                         | 8.4             | H                        | 0.4                     | 0.4                      |
|       | 15-30              | 10 yr 6/3                     | 3.4                                          | 84.5 9.9 5.6                              | LSa                        | 5.4 2.2 3.2                                   | 0 7 41                                         | 8.5             | H                        | 0.3                     | 0.3                      |
|       | 30-90              | 10 yr 6/2.5                   | 4.7                                          | 95.6 1.8 2.6                              | Sa                         | 3.1 0.7 2.4                                   | 0 6 14                                         | 8.5             | H                        |                         |                          |
| 55    | 0-6                | 7.5 yr 4/2                    | 0.0                                          | 77.9 16.3 5.8                             | LSa                        | 18.6 7.9 10.7                                 | ½ 2 107                                        | 7.6             | L                        | 0.6                     | 4.3                      |
|       | 6-18               | 10 yr 6/2                     | 1.6                                          | 74.9 18.3 6.8                             | SaL                        | 10.0 3.7 6.3                                  | 0 6 80½                                        | 8.2             | VL                       | 0.1                     | 0.0                      |
|       | 18-36              | 10 yr 5.5/3                   | 4.1                                          | 85.0 8.3 6.7                              | LSa                        | 7.8 2.2 5.6                                   | ½ 10 47                                        | 8.4             | L                        | 0.1                     | 0.0                      |
|       | 36-90              | 10 yr 6/2                     | 4.3                                          | 94.5 2.9 2.6                              | Sa                         | 3.8 0.9 2.9                                   | ½ 4½ 16                                        | 8.6             | M                        |                         |                          |
| 56    | 0-5                | 10 yr 3.5/2                   | 0.0                                          | 57.7 37.1 5.2                             | SaL                        | 22.3 8.5 13.8                                 | 1 2½ 222                                       | 8.2             | H                        | 2.4                     | 3.4                      |
|       | 5-15               | 10 yr 5/3                     | 0.2                                          | 74.3 19.0 6.7                             | SaL                        | 9.6 4.2 5.4                                   | 0 1 82                                         | 8.5             | M                        | 0.1                     | 0.0                      |
|       | 15-90              | 10 yr 6/2.5                   | 0.2                                          | 92.3 3.1 4.6                              | SaL                        | 3.9 1.0 2.9                                   | 0 3½ 22                                        | 8.7             | L                        | 0.4                     | 0.1                      |
| 57    | 0-6                | 10 yr 3.5/2                   | 0.1                                          | 58.7 36.8 4.5                             | SaL                        | 22.0 9.3 12.7                                 | 0 ½ 142                                        | 8.1             | H                        | 2.6                     | 3.4                      |
|       | 6-18               | 10 yr 6/3                     | 0.6                                          | 75.0 19.0 6.0                             | SaL                        | 12.8 2.0 10.8                                 | ½ ½ 57                                         | 8.5             | M                        | 0.7                     | 0.1                      |
|       | 18-33              | 10 yr 6/4                     | 0.1                                          | 88.5 6.7 4.8                              | Sa                         | 4.5 1.8 2.7                                   | ½ 0 29½                                        | 8.6             | M                        | 0.3                     | 0.3                      |
|       | 33-60              | 10 yr 6/2.5                   | 5.6                                          | 88.9 5.0 6.1                              | Sa                         | 5.3 1.8 3.5                                   | 0 0 18                                         | 8.8             | M                        |                         |                          |
|       | 60-90              | 10 yr 5.5/2                   | 12.0                                         | 95.9 1.4 2.7                              | Sa                         | 5.3 0.6 2.7                                   | 0 ½ 12                                         | 8.9             | M                        |                         |                          |
| 58    | 6 ) 0-6            | 2.5 yr 3.5/2                  | 3.3                                          | 69.5 26.3 4.2                             | SaL                        | 24.2 14.2 10.0                                | 2½ 4½ 234                                      | 6.9             | O                        | 0.0                     | 4.9                      |
|       | to ) at 30         | 5 yr 4/2                      | 4.2                                          | 68.5 24.3 7.2                             | SaL                        | 17.1 7.8 9.3                                  | 1½ 2½ 111                                      | 7.2             | O                        | 0.0                     | 1.6                      |
|       | 90 ) at 76         | 2.5 yr 4.5/2.5                | 3.2                                          | 69.5 23.9 6.6                             | SaL                        | 14.9 6.2 8.7                                  | ½ 2 59                                         | 7.8             | O                        |                         |                          |





| Stand | Horizon<br>(cm)                                 | Munsell <sup>1,2</sup><br>colour                       | Gravel<br>%                 | Texture,<br>Sand Silt Clay                                       | Text. <sup>2,3</sup><br>class | Moisture<br>FC               | Char.,<br>PWP              | % <sup>2,4</sup><br>AW     | Avail. Nutrients, ppm. <sup>2,5</sup><br>N P K | pH <sup>2</sup>   | Free <sup>2,6</sup><br>Lime | Inorg. <sup>2,7</sup><br>% | Organic <sup>2,7</sup><br>% |
|-------|-------------------------------------------------|--------------------------------------------------------|-----------------------------|------------------------------------------------------------------|-------------------------------|------------------------------|----------------------------|----------------------------|------------------------------------------------|-------------------|-----------------------------|----------------------------|-----------------------------|
| 59    | 0 ) at 2<br>to ) at 23                          | 5 yr 4/2<br>5 yr 4.5/2                                 | 3.0<br>2.7                  | 59.5 36.4 4.1<br>61.0 34.3 4.7                                   | SaL<br>SaL                    | 28.8<br>20.3                 | 13.9<br>7.3                | 14.9<br>13.0               | 5 3½ 213<br>1½ 2 127                           | 7.2<br>7.5        | O<br>O                      | 0.0<br>0.0                 | 4.7<br>2.2                  |
|       | 66 ) at 60<br>66-90                             | 5 yr 5/2.5<br>5 yr 5.5/2                               | 7.7<br>26.5                 | 67.7 23.4 8.9<br>72.4 18.1 9.5                                   | SaL<br>SaL                    | 14.1<br>10.3                 | 5.5<br>4.2                 | 8.6<br>6.1                 | ½ 2 127<br>1 0 66½                             | 7.9<br>8.2        | O<br>M                      | 0.0<br>0.0                 | 1.1                         |
| 60    | 20 ) 0-20<br>to ) at 30                         | 5 yr 3/2<br>5 yr 4.5/2                                 | 2.6<br>3.4                  | 65.8 29.0 5.2<br>60.5 28.8 10.7                                  | SaL<br>SaL                    | 29.5<br>18.3                 | 17.0<br>7.5                | 12.5<br>10.8               | 1½ 4 187<br>½ 1 78                             | 6.8<br>7.6        | O<br>O                      | 0.0<br>0.0                 | 5.5<br>2.0                  |
|       | 66 ) at 60<br>66-90                             | 5 yr 5/2<br>5 yr 5/2.5                                 | 6.8<br>31.7                 | 68.6 23.1 8.3<br>74.7 16.2 9.1                                   | SaL<br>SaL                    | 14.1<br>11.3                 | 5.8<br>4.4                 | 8.3<br>6.9                 | ½ 1 55<br>0 ½ 49                               | 8.0<br>8.3        | T<br>L                      | 0.0<br>0.0                 | 1.0                         |
| 61    | 0-10<br>10-13 <sup>8,13</sup><br>13-41<br>41-90 | 5 yr 3.5/1.5<br>5 yr 3/1<br>5 yr 4.5/1.5<br>5 yr 4.5/2 | 16.4<br>3.8<br>15.0<br>11.2 | 74.1 19.7 6.2<br>61.0 34.3 4.7<br>77.7 14.5 7.8<br>76.1 15.0 8.9 | SaL<br>SaL<br>SaL<br>SaL      | 23.6<br>56.5<br>13.7<br>13.7 | 10.5<br>36.3<br>5.8<br>6.2 | 13.1<br>20.2<br>7.9<br>7.5 | 1 2 84<br>½ 3½ 51<br>1½ 3 57                   | 8.0<br>7.8<br>7.8 | VL<br>O<br>O                | 0.0<br>0.0<br>0.0          | 4.6<br>11.1<br>1.7          |
| 62    | 0-5<br>5-18<br>18-90                            | 5 yr 4/2<br>5 yr 3.5/2<br>5 yr 4.5/2.5                 | 4.3<br>52.5<br>70.3         | 69.8 25.6 4.6<br>88.4 8.8 2.8<br>93.8 3.5 2.7                    | SaL<br>Sa<br>Sa               | 17.5<br>10.5<br>5.8          | 8.6<br>7.2<br>3.4          | 8.9<br>3.3<br>2.4          | 2½ 4½ 144<br>2½ 3½ 84<br>1 1 47                | 7.6<br>7.7<br>8.0 | O<br>O<br>VL                | 0.0<br>0.0                 | 2.4<br>2.4                  |
| 63    | 0-8<br>8-20<br>20-90                            | 5 yr 3/2<br>5 yr 3.5/2<br>2.5 yr 4.5/2.5               | 10.0<br>34.2<br>58.4        | 66.9 30.1 3.0<br>74.2 20.8 5.0<br>91.5 4.3 4.2                   | SaL<br>SaL<br>Sa              | 23.0<br>15.6<br>6.1          | 13.6<br>8.2<br>3.7         | 9.4<br>7.4<br>2.4          | 1 3½ 127<br>1 3 88<br>½ 2½ 61                  | 6.7<br>7.0<br>7.9 | O<br>O<br>VL                | 0.0<br>0.0                 | 4.8<br>1.6                  |
| 64    | 0-6<br>6-23<br>23-90                            | 5 yr 2.5/2<br>5 yr 3.5/2<br>5 yr 4/2.5                 | 13.5<br>51.7<br>58.8        | 66.9 29.3 3.8<br>79.1 16.3 4.6<br>91.1 5.1 3.8                   | SaL<br>LSa<br>Sa              | 30.4<br>13.7<br>7.1          | 19.6<br>7.0<br>3.5         | 10.8<br>6.7<br>3.6         | 6 8 256<br>1½ 4½ 142<br>½ 4 70½                | 6.5<br>6.0<br>6.2 | O<br>O<br>O                 | 0.0<br>0.0                 | 8.1<br>2.5                  |
| 65    | 0-10<br>10-23<br>23-90                          | 5 yr 2/2<br>5 yr 3/2<br>5 yr 4/2.5                     | 20.9<br>58.3<br>73.9        | 71.4 26.7 1.9<br>77.0 18.8 4.2<br>84.3 11.3 4.4                  | SaL<br>LSa<br>LSa             | 26.0<br>15.3<br>10.6         | 16.0<br>18.8<br>5.5        | 10.0<br>6.5<br>5.1         | 3½ 6 226<br>0 4 136<br>0 3 74½                 | 6.2<br>6.0<br>6.2 | O<br>O<br>O                 | 0.0<br>0.0                 | 7.3<br>3.3                  |
| 66    | 0-15<br>15-25<br>25-90                          | 5 yr 2/1.5<br>5 yr 3.5/2.5<br>5 yr 4/2.5               | 11.8<br>25.9<br>47.7        | 69.2 26.8 4.0<br>73.7 17.5 8.8<br>87.0 6.6 6.4                   | SaL<br>SaL<br>LSa             | 21.9<br>16.7<br>9.1          | 12.9<br>7.2<br>3.9         | 9.0<br>9.5<br>5.2          | 0 4½ 170<br>0 3½ 136<br>0 4½ 43                | 5.5<br>5.5<br>5.8 | O<br>O<br>O                 | 0.0<br>0.0                 | 5.1<br>1.8                  |
| 67    | 0-6<br>6-18<br>18-90                            | 5 yr 2/2<br>5 yr 3.5/2<br>5 yr 4/2.5                   | 15.3<br>45.1<br>65.2        | 68.8 29.3 1.9<br>81.3 14.1 4.6<br>88.0 7.4 4.6                   | SaL<br>LSa<br>Sa              | 27.8<br>15.9<br>11.4         | 17.5<br>7.7<br>5.3         | 10.3<br>8.2<br>6.1         | ½ 7 234<br>0 4 130<br>0 3½ 53                  | 6.4<br>6.1<br>6.6 | O<br>O<br>O                 | 0.0<br>0.0                 | 8.3<br>3.5                  |
| 68    | 0 ) at 5<br>to ) at 25<br>90 ) at 51            | 2.5 yr 2.5/3.5<br>2.5 yr 3.5/2.5<br>2.5 yr 3.5/2.5     | 27.6<br>66.1<br>57.0        | 72.6 24.5 2.9<br>84.9 10.4 4.7<br>93.6 3.0 3.4                   | SaL<br>LSa<br>Sa              | 23.5<br>15.2<br>8.8          | 14.4<br>6.3<br>3.7         | 9.1<br>8.9<br>5.1          | 1½ 7 201<br>0 3½ 68½<br>½ 2½ 45                | 6.1<br>6.2<br>7.2 | O<br>O<br>O                 | 0.0<br>0.0                 | 7.7<br>2.3                  |



| Stand | Horizon<br>(cm) | Munsell <sup>1,2</sup><br>colour |            | Gravel<br>% | Texture, % <sup>2</sup> |      |      | Text. <sup>2,3</sup><br>class | Moisture<br>FC | Char., % <sup>2,4</sup> |      | Avail. Nutrients, ppm. <sup>2,5</sup> |    |      |                 | Free <sup>2,6</sup><br>Lime | Inorg. <sup>2,7</sup><br>% | Organic <sup>2,7</sup><br>% |
|-------|-----------------|----------------------------------|------------|-------------|-------------------------|------|------|-------------------------------|----------------|-------------------------|------|---------------------------------------|----|------|-----------------|-----------------------------|----------------------------|-----------------------------|
|       |                 |                                  |            |             | Sand                    | Silt | Clay |                               |                | PWP                     | AW   | N                                     | P  | K    | pH <sup>2</sup> |                             |                            |                             |
| 69    | 0-8             | 5                                | yr 2/2     | 11.3        | 69.4                    | 27.6 | 3.0  | SaL                           | 27.2           | 15.6                    | 11.6 | 0                                     | 5½ | 208  | 6.0             | O                           | 0.0                        | 6.5                         |
|       | 8-25            | 5                                | yr 3.5/2   | 46.8        | 72.6                    | 24.3 | 3.1  | SaL                           | 20.6           | 10.6                    | 10.0 | 0                                     | 3½ | 158  | 6.1             | O                           | 0.0                        | 3.7                         |
|       | 25-48           | 5                                | yr 5/3     | 32.8        | 51.7                    | 36.5 | 11.8 | L                             | 22.7           | 5.8                     | 16.9 | 0                                     | 1  | 64½  | 6.9             | O                           |                            |                             |
|       | 48-90           | 5                                | yr 6/2     | 33.3        | 55.2                    | 31.7 | 13.1 | SaL                           | 13.9           | 2.6                     | 11.3 | 0                                     | 1  | 27½  | 8.1             | H                           |                            |                             |
| 70    | 0-10            | 2.5                              | yr 2/1.5   | 37.1        | 76.8                    | 19.5 | 3.7  | LSa                           | 22.6           | 14.8                    | 7.8  | 0                                     | 6  | 189  | 6.0             | O                           | 0.0                        | 5.7                         |
|       | 10-36           | 2.5                              | yr 3/2     | 37.6        | 80.8                    | 14.9 | 4.3  | LSa                           | 13.8           | 6.9                     | 6.9  | 0                                     | 3½ | 55   | 6.1             | O                           | 0.0                        | 2.5                         |
|       | 36-90           | 2.5                              | yr 3/2     | 40.8        | 85.2                    | 9.5  | 5.3  | LSa                           | 10.8           | 5.0                     | 5.8  | Q                                     | 3½ | 43   | 6.3             | O                           |                            |                             |
| 71    | 0-25            | 5                                | yr 1.7/1.5 | 20.3        | 70.2                    | 24.9 | 4.9  | SaL                           | 28.6           | 15.4                    | 13.2 | 0                                     | 6  | 258  | 5.8             | O                           | 0.0                        | 7.3                         |
|       | 25-48           | 5                                | yr 2/2     | 24.2        | 74.5                    | 17.2 | 8.3  | SaL                           | 16.4           | 7.9                     | 8.5  | 0                                     | 6  | 144½ | 5.7             | O                           | 0.0                        | 2.9                         |
|       | 48-90           | 5                                | yr 3.5/2.5 | 19.9        | 70.6                    | 17.1 | 12.3 | SaL                           | 17.3           | 6.4                     | 10.9 | o                                     | 6  | 96   | 5.9             | O                           |                            |                             |

Footnotes: <sup>1</sup> - HUE VALUE/CHROMA on air dry soil, using the "Revised Soil Colour Charts" of M. OYAMA and H. TAKEHARA (1967) based on the Munsell Colour Charts.

<sup>2</sup> - In the less than 2 mm fraction.

<sup>3</sup> - Sa = sand, Si = silt, C = clay, L = loam; e.g. SaL = sandy loam.

<sup>4</sup> - FC = Field Capacity, PWP = Permanent Wilting Percentage, AW = Available water = FC - PWP.

<sup>5</sup> - N = nitrogen, P = phosphorus, K = potassium.

<sup>6</sup> - T = trace, L = low, M = medium, H = high, VH = very high.

<sup>7</sup> - Inorganic and Organic carbon estimates, on 1968 samples only (Stands 52-71).

<sup>8</sup> - Sample inadequate to complete analysis.

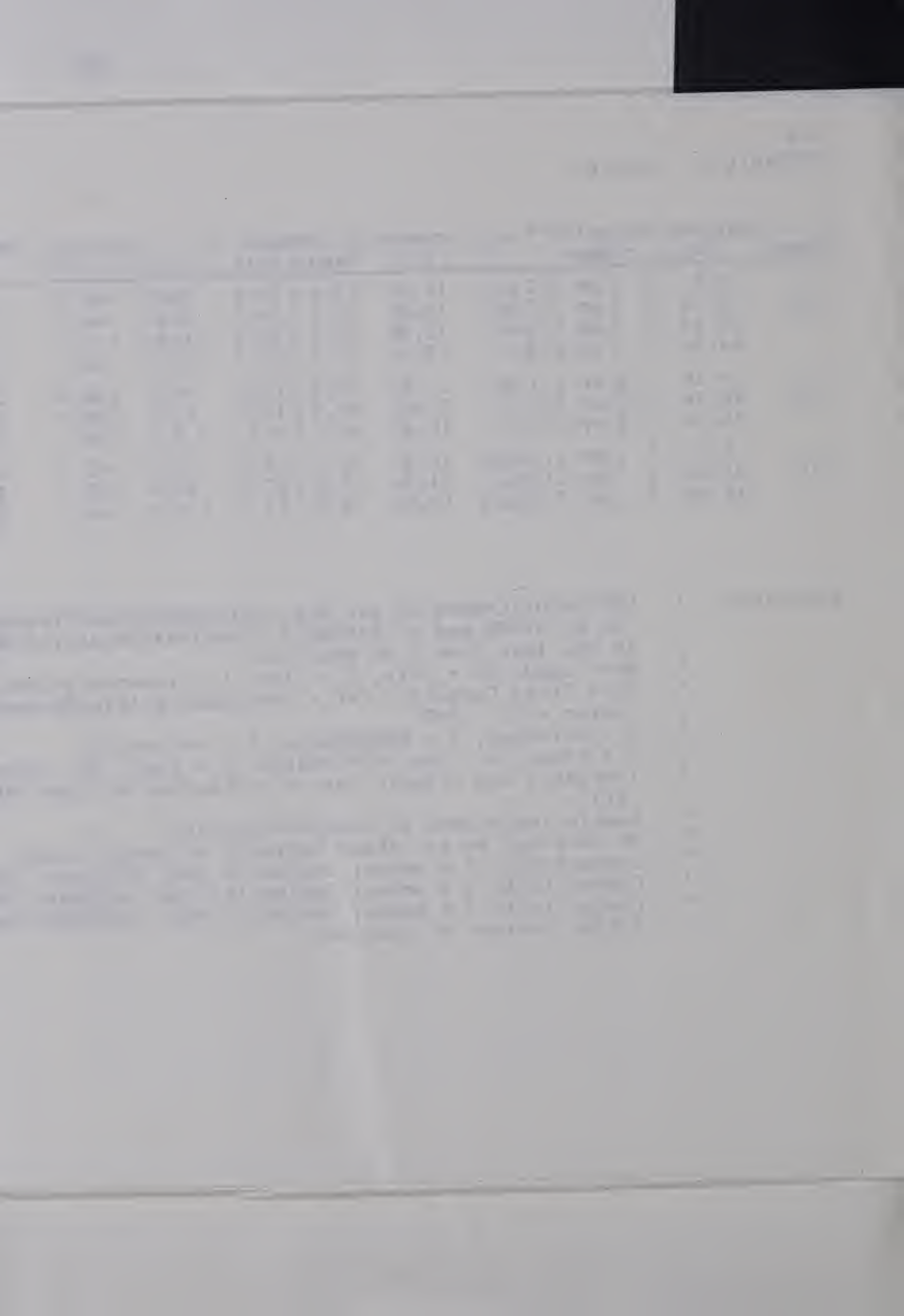
<sup>9</sup> - BC horizon; mostly shale bedrock; no sample taken.

<sup>10</sup> - Conductivity 1.8 mmhos; Sodium 42 ppm; Sulphate "low".

<sup>11</sup> - Conductivity 3.4 mmhos; Sodium 103 ppm; Sulphate "very high".

<sup>12</sup> - Conductivity 3.4 mmhos; Sodium 93 ppm; Sulphate "very high".

<sup>13</sup> - A high content of charcoal.





## APPENDIX 10

DETAILS OF RESOLUTION LEVELS IN THE  
CLUSTER ANALYSIS OF 71 STANDS

The meaningful levels of resolution for the Waterton group were Nos. 2, 11 and 12 (Fig. 14), level 2 giving a very stable configuration, *i.e.*, it did not change until level 8. This configuration was composed of a large cluster of 14 stands (Nos. 6, 7, 8, 18, 19, 20, 63-70) and six two-stand clusters, three of which were linked to the larger cluster. Most of the remaining Waterton stands were satellites of the large cluster. A satellite has a relatively high similarity to one or more members of an already existing cluster without, however, being admissible as a member of it. These satellites, together with the linked two-stand clusters, were absorbed into the larger cluster at much lower levels of resolution (levels 9 and 10) until, at level 11, all Waterton stands except Nos. 9, 10, 60 and 61 were absorbed. Stands 9 and 60 were absorbed at level 12, leaving a solitary 2-stand cluster (stands 10 and 61) linked to the main 32-stand cluster.

The most meaningful levels of resolution for the Banff-Jasper group were Nos. 3, 8 and 11 (Fig. 14). At level 3, the configuration was composed of a large cluster of 11 stands (Nos. 35, 36, 38, 42, 43, 45, 47, 49, 52, 53, 56), three smaller clusters (21, 30, 31; 40, 46; 54, 55, 57), six satellite stands of these four clusters and a



residual group of 14 unrelated stands. At level 8, one of the three smaller clusters (that of Nos. 54, 55 and 57), and five of the satellites (Nos. 32, 37, 39, 44, 48) were absorbed into the large cluster, but the rest of the stands were unchanged. At level 11, two more stands, 27 and 28, were drawn into the large cluster and stand 33 was added to the 21-30-31 cluster, the latter being linked to the large cluster also. Cluster 40-46 remained independent; ten stands were left as unrelated single stand clusters, *i.e.*, (Nos. 22-26, 29, 34, 41, 50 and 51).

These 10 unrelated stands included Nos. 23-26, the "high elevation" group detected on the ordination field. The failure of the cluster analysis to detect this group was thought to be due to the value of "BEGIN" used; within this group of four stands, all interstand similarities were less than 0.50 and therefore the cluster never started to form.

To try to detect loose clusters of this type, it was decided to repeat the cluster analysis, changing the "BEGIN" value to 0.25. This started the clustering at a much lower level of resolution, resulted in a considerable simplification of the configurations and left no stands unrelated.

As before, the Waterton stands and the Banff-Jasper stands were completely separate.

The most meaningful levels of resolution for the Waterton group were now 1, 3 and 9, especially 3 (Fig. 16). At level 1, all but six stands were included in the main



cluster. The six remaining stands were split into a cluster of four (Nos. 9, 58, 59 and 60) which was linked to the main cluster, and a cluster of two (Nos. 10 and 61) which was linked to the 4-stand cluster. At level 3, the configuration was extremely stable, stands 58 and 59 being now included in the main group and stands 9 and 60, and 10 and 61 forming two 2-stand groups, linked in turn to the main cluster. At level 9, stands 9 and 60 were taken into the main cluster, leaving the cluster of 10 and 61 directly linked to it.

For the Banff-Jasper group, the most important levels were 1 and 10 and, to a lesser extent, 8 (Fig. 16). At level 1, the configuration is composed of a large group of 19 stands, all but two of them being in Jasper (Nos. 32, 35-39, 42-45, 47-49, 52-57) and four smaller clusters (Nos. 21, 30, 31, 33; 23, 25, 34, 50; 24, 26; 40, 46), with all five clusters being linked to one another either directly or through satellites. The remaining six stands were satellites of either the large group or group 21-30-31-33. No further changes occurred in clustering with level 8, where stand Nos. 27 and 28 were taken into the large cluster, leaving only four satellite stands. At level 10, three of these remaining satellites, *i.e.*, Nos. 29, 41, 51, together with cluster 21-30-31-33 were absorbed into the large group and the fourth (No. 22) was taken into cluster 23-25-34-50. All three of the remaining smaller clusters were directly linked to the main one.

There was considerable agreement between the two cluster analyses. Changing the "BEGIN" value to 0.25 detected two extra clusters (22, 23, 25, 34, 50; 24, 26), both of which were left





as unrelated stands in the first cluster analysis. No stands have been left unrelated to the rest in the second analysis. At the same time, a great deal of sensitivity was lost, since both large clusters were made larger and therefore less tight at level 1.





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